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## *Toxoplasma gondii* in Circumpolar People and Wildlife

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# *Toxoplasma gondii* in Circumpolar People and Wildlife

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## Abstract

Despite extensive worldwide surveillance in populations of both people and wildlife, relatively little is known about *Toxoplasma gondii* ecology in the circumpolar north. Many northern animals and people demonstrate exposure to *T. gondii*, but the apparent low densities of domestic or wild felids suggest that additional transmission mechanisms are responsible for *T. gondii* persistence in high latitudes, whether remote source (from another region), vertical, or dietary. People in these northern communities who practice subsistence hunting might have an increased infection risk due to traditional food preparation techniques and frequent handling of wild game. Recent advances in *T. gondii* genotyping, understanding of host–parasite relationships, and increased human and wildlife surveillance will help to address knowledge gaps about parasite evolution, distribution, and abundance throughout the Arctic and Subarctic.

**Key Words:** Epidemiology—Parasitology—Toxoplasma—Transmission—Zoonotic.

## Introduction

FIRST DETECTED OVER A CENTURY AGO, the coccidian *Toxoplasma gondii* remains a pathogen of significant public health and ecological concern. This ubiquitous parasite infects a large number of vertebrate (mammalian and avian) intermediate host species and has a cosmopolitan distribution. Despite serologic evidence demonstrating widespread exposure to *T. gondii* in northern wildlife and people, transmission mechanisms in the circumpolar north remain unclear. The apparent low density of felid definitive hosts in the high Arctic indicates a need to better understand *T. gondii* ecology, particularly transmission. By identifying these pathways in the north, risks for wildlife populations and human health in arctic and subarctic ecosystems can be better mitigated. This review will summarize what is currently known about *T. gondii* in circumpolar human and wildlife populations and identify knowledge gaps that might be addressed in future research.

The life cycle of *T. gondii* is complex. Three infectious stages are known: oocysts, tachyzoites, and bradyzoites within tissue cysts. As the only known definitive hosts, infected felids support sexual reproduction of the parasite and excrete unsporulated oocysts in their feces (Frenkel et al. 1970). Intermediate hosts become infected via consumption of sporulated

oocysts in the environment or cysts in tissues of intermediate hosts (Weinman and Chandler 1954, Dubey et al. 1970, 1996). The parasite can be transmitted vertically when tachyzoites infect the fetus transplacentally, or horizontally when bradyzoites are ingested via carnivory or cannibalism (Beverley 1959). Once introduced into a food web, *T. gondii* can be maintained through trophic interactions and ongoing vertical transmission (Smith 2009). This transmission cycle is perpetuated only by asexual reproduction and is significant because it might cause *T. gondii* persistence in ecological communities, such as the Arctic, in which definitive hosts are infrequent, at low densities, or absent.

Because *T. gondii* replicates both sexually and asexually, recombinant and clonal isolates exist (Sibley et al. 2009). Three clonal lineages (I, II, and III) were identified through the study of European and North American isolates (Howe and Sibley 1995). Infection with Type II lineage represents the majority of human clinical toxoplasmosis cases. The Type II strain was more often present in recrudescing infections, especially in AIDS patients, whereas the Type I strain was typically associated with human congenital toxoplasmosis (Howe and Sibley 1995). Domestic animal infections in the United States and Europe are typically characterized as Types II and III strains (Dubey et al. 2004a). A fourth genotype, Type X, was originally isolated from sea otters and is similar to the Type II

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genotype (Miller et al. 2004, Khan et al. 2007). As *T. gondii* genotyping extends to samples from unstudied geographic regions, researchers report an increasing number of atypical strains with newly identified alleles (Dubey et al. 2007, Parmeswaran et al. 2010). Currently, few published reports exist describing the genomics of circumpolar *T. gondii* isolates, although such information would be useful in ecosystem and population level transmission studies, or to examine host susceptibility.

Most reports of *T. gondii* in wildlife are from serosurveys. Although serology is a useful method for documenting exposure to *T. gondii* in both animal and human populations, interpretation of wildlife results can be difficult due to a lack of validated tests and biologically relevant reference titers (Wobeser 2007). Several tests are commercially available and have been validated for swine, domestic cats, or people, but little to no information exists for the validity of these tests for wildlife. Given the potential for significantly different immune responses between species, determining a positive cut-off value for tests is difficult. This might ultimately lead to biased results or unreliable interpretations (Wobeser 2007). Because serosurveys are a common tool to detect exposure to *T. gondii*, efforts to improve species-specific serological methods would be useful for future research. Another limitation of serosurveillance is inadequate test sensitivity. In a study of congenital transmission of *T. gondii* in deer mice, 9 of 30 vertically infected offspring were *T. gondii*-positive by tissue polymerase chain reaction (PCR), but all mice were seronegative (Rejmanek et al. 2010). These data indicate that serological methods may be of limited value in the detection of some cases of vertical transmission (Rejmanek et al. 2010). Utilizing multiple testing methods, such as performing both tissue PCR and serology, is sometimes done and may be a useful cross-referencing procedure (Dubey 2009). Although these assays identify different endpoints (DNA vs. antibodies, respectively), comparing the results from multiple detection methods might be useful for interpreting ambiguous results.

### ***T. gondii* in Arctic and Subarctic Wildlife**

People dwelling in the arctic and subarctic regions of the world often depend on stable, healthy populations of wildlife for subsistence and livelihood. Wildlife species such as caribou (*Rangifer tarandus*), walrus (*Odobenus rosmarus*), and seal species (*Erignathus barbatus*, *Pusa hispida*, and *Halichoerus grypus*) have high cultural and economic value, providing nutrition and raw materials to support a subsistence lifestyle for circumpolar communities. The frequent contact between people and wildlife in northern regions increases the risk of zoonotic infection and serosurveys have identified exposure to *T. gondii* in a range of arctic and subarctic wildlife species (Table 1). While *T. gondii* is a pathogen of concern in people, it might also have a negative impact on wildlife populations on which northerners depend, in part because of population impacts of pathogen-related abortion and congenital disease. Toxoplasmosis in some wildlife species might also additively influence population declines, often triggered by other anthropogenic and environmental pressures (Kutz et al. 2000, Vors and Boyce 2009).

In much of the Arctic and Subarctic, definitive hosts for *T. gondii* are not consistently present (Zarnke et al. 2000, Kutz et al. 2001, Messier et al. 2009). The sole felid ranging in the

northern latitudes is the lynx (*Lynx canadensis*), which is primarily limited to the boreal regions. Lynx as a definitive host remains unsubstantiated, although seropositive animals have been reported (Table 1) (Labelle et al. 2001, Zarnke et al. 2001). A closely related felid, the bobcat (*Lynx rufus*), shed oocysts following experimental infection, although shedding intensity was lower than in experimentally infected domestic cats (Miller et al. 1972). Lynx are reported throughout interior Alaska at relatively low population densities (Stieve et al. 2010). Domestic cats are not commonly kept as pets in northern communities, making it unlikely for cats to constitute a significant source of oocysts (Messier et al. 2009). On Svalbard, Norway, domestic cats are prohibited, although the village of Barentsburg has a limited indoor cat population (Prestrud et al. 2008). Thus, arctic and subarctic wildlife exposure to *T. gondii* is probably not solely driven by contact with oocysts in the terrestrial environment.

### **Ungulates**

Barren-ground caribou (*Rangifer tarandus groenlandicus*) are widely distributed across the Canadian Arctic and Subarctic and migrate annually between northern calving grounds, where they spend the summer, and more southern overwintering grounds (Kutz et al. 2001). Seroprevalence was higher in mainland caribou than in island caribou, possibly because the mainland caribou migrate below the timberline, where they are more likely to encounter oocysts from felids (Kutz et al. 2001). This trend is similar in muskox (*Ovibos moschatus*) in northern Canada, where *T. gondii* seroprevalence was higher on the mainland where this species co-occurs with some felids than on arctic islands (Kutz et al. 2000). No differences in exposure were detected between males and females in either species (Kutz et al. 2001).

Exposure to *T. gondii* has also been reported in Alaskan ungulates. Antibodies against *T. gondii* were detected in Dall sheep (*Ovis dalli*), caribou (*R. tarandus*), and moose (*Alces alces*) from the Alaskan interior and northwestern regions (Zarnke et al. 2000, Stieve et al. 2010). Stieve et al. (2010) reported *T. gondii* antibodies in 0.4% of 452 Alaskan caribou, which differed from a previous report of 6% seroprevalence in similar geographic locations (Zarnke et al. 2000), although the method of detection was not the same (Table 1). In the more recent study, although 2 of 189 adult caribou were seropositive for *T. gondii*, no antibodies were detected in another 216 animals that were <1-year-old (Stieve et al. 2010). It is possible that some caribou calves infected with *T. gondii* are stillborn or preyed upon by wolves early in life and never reach adulthood.

Semicaptive reindeer (*R. tarandus*) in Fennoscandia are conspecific with caribou and susceptible to toxoplasmosis. Two yearling *R. tarandus* developed severe enteritis when intrarumenally inoculated with *T. gondii* oocysts (Oksanen et al. 1996). Tissues from one of these *R. tarandus* demonstrated acute necrotizing lymphadenitis in the mesenteric lymph nodes and tachyzoites were present in the mesenteric lymph nodes and small intestinal wall (Oksanen et al. 1996). Serologic evidence of *T. gondii* exposure was also documented in *R. tarandus* from Finland and Norway (Table 1) (Oksanen et al. 1997). In this study, seroprevalence was correlated with increasing age and winter corral feeding, which suggested that animals are continually exposed to *T. gondii* throughout

TABLE 1. SEROLOGIC EVIDENCE OF *TOXOPLASMA GONDII* IN ARCTIC AND SUBARCTIC WILDLIFE

Common name	Scientific name	Number tested	Prevalence (%)	Assay used	Country	Locality (if known)	Reference
Felids	Felidae						
Canada Lynx	<i>Lynx canadensis</i>	106	44.0	MAT	Canada	Quebec	Labelle et al. (2001)
		255	15.3	MAT	United States	Interior Alaska	Zarnke et al. (2001)
Eurasian Lynx	<i>Lynx lynx</i>	156	75.4	DAT	Sweden	North and Central Sweden	Ryser-Degiorgis et al. (2006)
Canids	Canidae						
Red Fox	<i>Vulpes vulpes</i>	29	31.0	DT	Norway/ Sweden	Not described	Kapperud (1978)
		8	12.5	MAT	United States	Alaska	Stieve et al. (2010)
Arctic Fox	<i>Vulpes lagopus</i>	260	66.9	DAT	Norway	Svalbard	Akerstedt et al. (2010)
		2	100.0	DT	Norway/ Sweden	Not described	Kapperud (1978)
		594	43.0	DAT	Norway	Svalbard	
		60	51.7	DAT	Norway	Svalbard	Akerstedt et al. (2010)
Wolf	<i>Canis lupus</i>	320	17.8	MAT	United States	Alaska	Stieve et al. (2010)
		97	18.6	DAT	Norway	Svalbard	Akerstedt et al. (2010)
		125	8.8	MAT	United States	Alaska	Zarnke et al. (2000)
Bears	Ursidae						
Grizzly Bear	<i>Ursus arctos</i>	480	18.0	LAT	United States	Alaska	Chomel et al. (1995)
	<i>U. arctos</i>	892	25.0	MAT	United States	Alaska	Zarnke et al. (1997)
Black Bear	<i>Ursus americanus</i>	40	15.0	LAT	United States	Alaska	Chomel et al. (1995)
	<i>U. americanus</i>	143	43.4	MAT	United States	Alaska	Zarnke et al. (2000)
Polar Bear	<i>Ursus maritimus</i>	419	20.1	MAT	Norway	Svalbard and Barents Sea	Oksanen et al. (2009)
		108	11.1	MAT	Greenland	Eastern Greenland	Oksanen et al. (2009)
		500	6.0	LAT	United States/ Russia	Beaufort and Chukchi Seas	Rah et al. (2005)
		228	45.6	DAT	Norway	Svalbard	Jensen et al. (2010)
		136	13.2	LAT	United States	Alaska	Kirk et al. (2010)
Pinnipeds	Phocidae						
Pacific Walrus	<i>Odobenus rosmarus</i>	53	5.6	MAT	United States	Alaska	Dubey et al. (2003)
Harbor Seal	<i>Phoca vitulina</i>	311	16.4	MAT	United States	Alaska	Dubey et al. (2003)
		34	8.8	MAT	Canada	Metis-sur-mur and Bic	Measures et al. (2004)
Hooded Seal	<i>Cystophora cristata</i>	60	1.7	MAT	Canada	Gulf of St. Lawrence River and Estuary	Measures et al. (2004)
Grey Seal	<i>Halichoerus grypus</i>	122	9.0	MAT	Canada	Port Hood and Hay Island	Measures et al. (2004)
Walrus	Odobenidae <i>O. rosmarus</i>	17	6.0	DAT	Norway	Svalbard	Prestrud et al. (2007)
Rodents	Rodentia						
Norway Lemming	<i>Lemmus lemmus</i>	40	3.0	DT	Norway/ Sweden	Not described	Kapperud (1978)
Ungulates	Artiodactyla						
Dall Sheep	<i>Ovis dalli</i>	319	6.9	MAT	United States	Alaska	Zarnke et al. (2000)
Musk Ox	<i>Ovibos moschatus</i>	49	2.0	MAT	Canada	Victoria Island, Nunavut	Wu et al. (2010)
		203	6.4	MAT	Canada	Northwest Territories/ Nunavut	Kutz et al. (2000)
Caribou/ Reindeer	<i>Rangifer tarandus</i>	241	6.6	MAT	United States	Alaska	Zarnke et al. (2000)
		452	0.4	MAT	United States	Alaska	Stieve et al. (2010)
		104	2.9	IHAT	Canada	Northwest Territories	Johnson et al. (2010)
		2577	0.9	DAT	Finland/ Norway	In Norway: Finnmark County	Oksanen et al. (1997)
		147	29.1	MAT	Canada	Northwest Territories/ Nunavut	Kutz et al. (2001)
		866	1.0	DAT	Norway		Vikoren et al. (2004)
Red Deer	<i>Cervus elaphus</i>	99	12.0	DT	Norway/ Sweden	Not described	Kapperud (1978)
		571	7.7	DAT	Norway		Vikoren et al. (2004)
Roe Deer	<i>Capreolus capreolus</i>	199	34.0	DAT	Sweden	Nationwide survey	Malmsten et al. (2011)
		760	33.9	DAT	Norway		Vikoren et al. (2004)
Moose	<i>Alces alces</i>	240	1.3	MAT	United States	Alaska	Zarnke et al. (2000)
		417	20.0	DAT	Sweden	Nationwide survey	Malmsten et al. (2011)
		2142	12.6	DAT	Norway		Vikoren et al. (2004)
Birds							
Barnacle Goose	<i>Branta leucopsis</i>	149	7.0	DAT	Norway	Svalbard	Prestrud et al. (2007)

MAT, modified agglutination test; DT, dye test; DAT, direct agglutination test; LAT, latex agglutination test; IHAT, indirect hemagglutination test.

life and infection is facilitated by feeding management style (Oksanen et al. 1997). Natural transplacental toxoplasmosis was documented in a stillborn *R. tarandus* fetus from a private farm in Texas (Dubey et al. 2002). The brain contained multifocal encephalitic lesions and focal necrosis was observed in the cotyledonary villi of the placenta. Additionally, tissue cysts were detected in the fetal cerebellum and serological testing of the dam revealed a high antibody titer to *T. gondii*, demonstrating that natural vertical transmission can result in clinical toxoplasmosis in *R. tarandus* (Dubey et al. 2002).

Low recruitment rates have been reported for several boreal caribou herds in northern Alberta, Canada (McLoughlin et al. 2003), and caribou populations in northwestern Alaska are at risk of decline due to habitat degradation and decreasing lichen abundance (Joly et al. 2009). Additionally, climate change might lead to an increase in snow depth, increase in storm frequency, and asynchrony between seasonal vegetation growth and caribou activities, thus affecting overall caribou health and population viability (Joly et al. 2009). Although it is unknown if *T. gondii* or another etiologic agent that reduces reproductive success is endemic in these populations, such information would be extremely valuable to explore the role of *T. gondii* in population declines of arctic wildlife.

#### Nonfelid carnivores

Antibodies to *T. gondii* have been detected in several arctic and subarctic carnivore species (Table 1). Reichard et al. (2008) first reported *T. gondii* antibodies in wolverines (*Gulo gulo*) from Nunavut, Canada. Wolverines are generally found above timberline where they are less likely to encounter *T. gondii* oocysts, but home range sizes are variable (100–900 km<sup>2</sup>) and might encompass land both above and below the timberline, thus increasing the likelihood for oocyst transmission opportunities from lynx (Reichard et al. 2008). Additionally, wolverines are generalist feeders and scavenge all types of carcasses, including wild ungulates such as muskox and caribou (Reichard et al. 2008). Given this type of feeding ecology, exposure to *T. gondii* might also be a consequence of ingesting bradyzoites from intermediate hosts. Wolverines are commonly harvested by Inuit hunters and might represent a public health risk to individuals who skin or otherwise handle carcasses (Reichard et al. 2008).

Arctic foxes (*Vulpes lagopus*) are circumpolar canids that feed opportunistically in both coastal and terrestrial environments (Prestrud et al. 2008). In Svalbard, migratory birds and scavenged *R. tarandus* carcasses comprise the diet of arctic fox (Prestrud et al. 2008), whereas in other arctic environments, fox diets consist largely of lemmings and voles (Audet et al. 2002). Additionally, oocysts are not an important factor in the transmission and maintenance of *T. gondii* on Svalbard as evidenced by an absence of antibodies in terrestrial herbivores in the ecosystem (Prestrud et al. 2007). Sorensen et al. (2005) detected disseminated toxoplasmosis in three dead arctic foxes and Prestrud et al. (2008) isolated viable *T. gondii* from arctic foxes in Svalbard, Norway, through bioassay in mice and cats. Multilocus genotyping revealed the isolate to be from the Type II clonal lineage, which is the predominant strain in Europe (Prestrud et al. 2008).

Migratory birds are a potential source of exposure, as they are an important prey item for arctic foxes. In Nunavut, Ca-

nada, foxes also supplement their diets with goose eggs when lemmings are scarce (Samelius et al. 2007). Barnacle geese (*Branta leucopsis*) and pink-footed geese (*Anser brachyrhynchus*) migrate seasonally between southern Europe and Svalbard and seropositive barnacle geese were found on Svalbard (Table 1) (Prestrud et al. 2007, 2008). Dubey et al. (2004b) isolated viable Type III *T. gondii* from brain tissue of one Canada goose (*Branta canadensis*), indicating that migratory waterfowl can be intermediate hosts for *T. gondii*. The role of migratory birds in pathogen transmission has been investigated for other pathogens, such as avian influenza virus (Brown and Stallknecht 2008) and West Nile virus (Peterson et al. 2003). Further examination of waterfowl in *T. gondii* transmission dynamics is warranted.

Little is known about exposure to *T. gondii* in other circumpolar canids, such as red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), and wolves (*Canis lupus*). No antibodies were detected in coyotes from Alaska, but seroprevalence in red foxes has been reported in multiple studies (Table 1) (Stieve et al. 2010). Stieve et al. (2010) and Zarnke et al. (2000) independently documented antibodies against *T. gondii* in gray wolves (*C. lupus*) from Alaska. Gray wolves mainly hunt caribou and other ungulates in the arctic and subarctic and these prey items are predicted to be sources of *T. gondii* exposure for canids. Stieve et al. (2010) detected lower seroprevalence in caribou (0.4%,  $n=452$ ) than in wolves (17.8%,  $n=320$ ), thus positing the existence of additional or alternative sources for wolf exposure. Unidentified or unexamined prey sources could be important sources of *T. gondii* for wolves, but the potential for vertical transmission might also be considered. Additionally, continued consumption of infected caribou might account for a bioaccumulation effect, leading to higher seroprevalence in wolves from consistent exposure.

A number of serosurveys document high levels of exposure to *T. gondii* in circumpolar bear species. Zarnke et al. (1997) examined sera from 892 grizzly bears (*Ursus arctos*) in Alaska by the modified agglutination test (MAT) and detected antibodies in 220 (24.7%). The bears were captured from northwestern, southern, and eastern interior Alaska and seroprevalence was highest in the northwestern bears. Geographic differences in prevalence are likely accounted for by differences in feeding ecology rather than exposure to oocysts, given the absence of both lynx and domestic cats at the northwestern collection sites (Zarnke et al. 1997). Recently, Dubey et al. (2010) isolated a new atypical *T. gondii* genotype from an asymptomatic, free-ranging black bear in southern Alaska, northwest of Anchorage. This is a significant finding, as very few *T. gondii* isolates have been collected from northern wildlife. The authors used 10 restriction fragment length polymorphism markers to reveal a genotype that was a combination of Type I, II, and III alleles at different loci (Dubey et al. 2010). Given the southern location and the forested habitat of this collection site, range overlap with the Canada lynx is likely; therefore, sexual reproduction of *T. gondii* within a definitive host might account for this new genotype.

Polar bear (*Ursus maritimus*) exposure to *T. gondii* is especially interesting, as this species has a feeding ecology that spans both terrestrial and marine ecosystems. Serosurveys reported antibodies against *T. gondii* in polar bears and their seal prey (Table 1) throughout the circumpolar north (Rah et al. 2005, Oksanen et al. 2009, Jensen et al. 2010). On

Svalbard, two primary prey species of polar bears, ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*), demonstrated serological evidence of exposure to *T. gondii* (Jensen et al. 2010). Dubey et al. (2003) reported seropositive samples from many marine species with widely varying feeding ecologies and distribution, including seals, sea lions, dolphins, and walruses (Table 1). Sporulated *T. gondii* oocysts persist in seawater for long periods of time (Lindsay and Dubey 2009). Additionally, relatively high seroprevalence levels in circumpolar marine mammals suggest the possibility of several transmission events and methods. Further study of the potential overlap of *T. gondii* genetic composition and ecology between marine and terrestrial environments in northern latitudes is needed to improve our understanding of pathogen flow in these wild ecosystems.

**T. gondii as a Public Health Concern in Northern Canada**

Although many human infections with *T. gondii* are sub-clinical or asymptomatic, the parasite can cause severe illness, especially in immunosuppressed and pregnant people (and their fetuses) (Jones et al. 2001, Dubey and Jones 2008). People acquire *T. gondii* infections both pre- and post-natally (Dubey and Jones 2008). Because toxoplasmosis is not a nationally notifiable disease in Canada, few reports exist to describe the prevalence of *T. gondii*. In Quebec, however, pregnant women are tested for *T. gondii* exposure through a provincial screening program, and, as a result, most epidemiological information from the Canadian north have been conducted in Nunavik (northern Quebec). The high seroprevalence of antibodies against *T. gondii* detected in women from this region is interesting because domestic cats and lynx are infrequent or absent, suggesting alternative mechanisms for *T. gondii* transmission, such as dietary, congenital, or remote source (originating from a different region) transmission (Messier et al. 2009). Traditionally prepared food items of animal origin are often eaten raw or partially cooked, and increasing serologic evidence of *T. gondii* exposure in arctic wildlife (terrestrial and marine) indicates that these animals are likely intermediate hosts for the parasite (Table 2). As a result, people in northern Canada and other circumpolar regions might have an increased risk of foodborne *T. gondii* infection and subsequent potential for congenital transmission (McDonald et al. 1990, Forbes et al. 2009, Messier et al. 2009). The seroprevalence data show that people in Inuit communities in northeastern Canada are routinely but variably ex-

posed to *T. gondii*, also substantiating a need for further investigation.

Additionally, chlorinated but unfiltered surface water is used as drinking water in most Inuit communities and an estimated 30% of Nunavik Inuit collect raw water from natural sources such as streams and lakes (Messier et al. 2009). Oocysts survive well in aquatic environments and are known to facilitate waterborne transmission, which occurs when contaminated sediments in water runoff are deposited in waterways or reservoirs (Bowie et al. 1997, Conrad et al. 2005, Jones and Dubey 2010). Explaining the presence of oocysts in a watershed requires an understanding of regional hydrology and potential or determined sources of oocysts.

McDonald et al. (1990) provided compelling evidence for congenital *T. gondii* infection in a group of Inuit women from the Ungava Bay region of northern Quebec (Nunavik). Serologic screening (by indirect fluorescent antibody test [IFAT]) of pregnant women in this region has been standard practice since 1982 and the estimated seroprevalence was ~50% in the 1980s and early 1990s (McDonald et al. 1990). In 1987, doctors reported seroconversion in four women during pregnancy, putting their offspring at risk of congenitally acquired toxoplasmosis. Although the women remained asymptomatic during pregnancy, one child was born with cerebral calcifications, choreoretinitis, a ventricular cyst, and a rising IgM titer, indicating an active *T. gondii* infection (McDonald et al. 1990). Infection in a second child was suspected due to a mild developmental delay, but follow-up serology was not performed; the remaining two children were apparently uninfected. This remains the best published account of probable congenital toxoplasmosis in Canadian Inuit, but the organism was not actually isolated from putatively infected individuals. As a follow-up, Lavoie et al. (2008) performed a chart review of 1006 pregnant women in Nunavik between 1994 and 2003, identifying 19 women who might have become infected and seroconverted during pregnancy (~2% incidence over a 10-year period). It is believed that at least two of these women were infected before pregnancy. Most of the seropositive women and their children were treated, and none of the children available for follow-up were diagnosed with congenital toxoplasmosis, indicating the usefulness of screening programs of this type, especially in high-risk populations (Lavoie et al. 2008).

Messier et al. (2009) selected data from a cross-sectional Nunavik Health Survey and estimated risk factors for permanent residents of Nunavik. Information about water

TABLE 2. SUMMARY OF RISK FACTORS IDENTIFIED FOR EXPOSURE TO *TOXOPLASMA GONDII* IN NORTHERN COMMUNITIES

Risk factors	Study region	Reference
Skinning animals	Ungava Bay, Nunavik Canada	McDonald et al. (1990)
Ingesting raw caribou, seal, and ptarmigan		
Hunting while pregnant		
Cleaning domestic water reservoirs	Nunavik, Canada	Messier et al. (2009)
Marine mammal, fish, and bird consumption		
Fishing		
Berry picking		
Bird handling		
Being female		
Increasing age	Alaska	Peterson et al. (1974)
Increasing age	Northern Quebec	Tanner et al. (1987)

treatment and sources, household demographics, cooking practices, typical foodstuffs handled or eaten, education level, personal income, and traditional activities were compared to seroprevalence (Messier et al. 2009). Several socio-demographic factors, such as age, gender, and participation in traditional activities all positively correlated with *T. gondii* seropositivity. Results indicated that exposure to *T. gondii* increased with age and frequency of fishing, berry picking, and bird handling (Table 2). Women were more frequently seropositive than men and seroprevalence negatively correlated with education level. Additionally, seroprevalence positively correlated with frequency of cleaning domestic water reservoirs and consumption of marine mammals (seal, walrus, and beluga), fish, and birds (Messier et al. 2009). The authors hypothesized that the frequent participation of women in traditional food and hide preparation leads to an increased risk for *T. gondii* exposure. Additionally, less educated individuals might not understand the need for sanitation practices, including hand washing and the cleaning of utensils (Messier et al. 2009). McDonald et al. (1990) identified similar risk factors for women (men were not included in the study). For example, Inuit women who participated in skinning animals, hunting while pregnant, regularly ingesting raw caribou meat, and ingesting seal and ptarmigan meat (especially livers), all showed elevated odds of *T. gondii* exposure (Table 2) (McDonald et al. 1990). Interestingly, Fromont et al. (2009) reported a strong household effect on *T. gondii* seroprevalence in rural France, implying that common risk factors within each household were responsible for the heterogeneity within a community. This finding suggests that community studies of *T. gondii* should explore the use of household serostatus as a sampling unit, rather than the serostatus of individuals.

A serological study of Eskimo, Aleut, Athabascan, and Tlingit communities in Alaska documented widespread *T. gondii* exposure, even north of the Arctic Circle, where few to no domestic cats or lynx were thought to exist (Peterson et al. 1974). The study compared human seroprevalence in cat-free regions to that of people in regions where domestic cats are kept and lynx are endemic. Overall *T. gondii* seroprevalence in 1188 Alaskan natives (616 females, 572 males) was 27.9% by IFAT and 16.4% by indirect hemagglutination test (Peterson et al. 1974), and increased with age (Table 2). Household cats were more common than originally thought, inhabiting most of the communities tested, including the far north. Due to this unexpected finding, a difference in *T. gondii* between cat and no-cat regions could not be determined. This study did, however, identify indigenous Alaskans as a newly recognized risk group. In an earlier survey, 20 Alaskan Eskimo were not seropositive for *T. gondii* (Feldman and Miller 1956, Peterson et al. 1974).

Because food preparation is highly correlated with the probability of *T. gondii* exposure, an attempt was made to determine *T. gondii* cyst infectivity following traditional country food preparation methods (Gajadhar et al. 2004, Forbes et al. 2009). Skin, blubber, and muscle from experimentally infected gray seals were used to prepare the following traditional foods: igunaq, nikku, and sausage (Gajadhar et al. 2004, Forbes et al. 2009). Igunaq is marine mammal skin and muscle that is traditionally buried in the ground, allowed to decompose and ferment for several months, and then eaten the next year. Nikku (dried skeletal muscle) and sausage were prepared from muscle tissue

(Forbes et al. 2009). The meats were bioassayed in cats at multiple stages of preparation and storage, with the diagnostic endpoints being oocyst recovery and MAT serology (Forbes et al. 2009). In a previous study, ingestion of *Toxoplasma*-infected seal tissues led to patent infections in cats when fed raw (Gajadhar et al. 2004). Although no cats in this study shed oocysts after eating the traditionally prepared meat, the highly variable conditions under which country foods are prepared do not completely eliminate risk of *T. gondii* transmission (Forbes et al. 2009). Additionally, northern strains of *T. gondii* in wildlife might be more resistant to freezing and traditional food preparation methods than the domestic swine isolate used in this study; another northern-adapted parasite, *Trichinella nativa*, is much more resistant to freezing than temperate adapted *Trichinella* species such as *T. spiralis* (Forbes et al. 2003, 2009). Further work is needed to determine the freeze susceptibility of Arctic strains of *T. gondii* in harvested wildlife.

### Future Directions

Despite the incredible repertoire of knowledge that has been gathered, there are still gaps in our understanding about sylvatic toxoplasmosis in the north. Advances in *T. gondii* genotyping hold promise for insight into the evolution of *T. gondii* in wildlife and will enable a better understanding of pathogen flow on both global and local scales. Although a low felid density in the Arctic limits the likelihood for sexual recombination of *T. gondii*, recombinant genotypes might be introduced to the north through other pathways, such as by migratory species, and then maintained asexually. Additionally, this more detailed genetic information might help to identify selection pressures within the host or environment that affect aspects of virulence or host susceptibility. Intermediate host susceptibility can vary with different prey items (Afonso et al. 2007) and with the infectious *T. gondii* stage. Dubey (2006) compared infectivity of oocysts and bradyzoites to mice and domestic cats, and found that oral administration of oocysts to mice is more likely to induce infection than oral oocyst administration in cats. Alternately, cats fed bradyzoites were more likely to develop patent infections than cats fed oocysts. Different strains of *T. gondii*, especially atypical genotypes, might not induce oocyst shedding in experimentally exposed domestic cats (Dubey et al. 2010). Possibly unrecognized host species, felid or other, might be more competent definitive hosts for atypical genotypes, or some genotypes might simply be maintained by asexual reproduction of the parasite.

Many northern wildlife species rely on carnivory in some form, whether scavenging or hunting. Arctic-adapted strains might be maintained through carnivory and congenital transmission and no longer require passage through a definitive host. To explore this hypothesis, attempts can be made to isolate and culture *T. gondii* from fresh tissues of Arctic wildlife. Subsequent laboratory experiments could aim to determine infectivity to cats, or other animals, through feeding trials. Isolation of organisms and/or DNA also allows the application of molecular tools to gain additional information on parasite phylogenetics, evolution, and host/parasite interactions. With the increasing number of diagnostic tools available, researchers have an opportunity to look beyond simple seroprevalence in wildlife studies. Additionally,

current serological methods should be validated for the species of concern whenever possible.

Over the first 100 years of *T. gondii* history, continual progress was made to understand the parasite's life cycle, transmission patterns, biology, molecular structure, and host range. In addition to ongoing molecular and microbiological research, future research will attempt to examine sylvatic *T. gondii* from a landscape level, enabling our understanding of parasite flow in a context that provides inference into *T. gondii* in the environment, wildlife, and people. Increased surveillance efforts focusing on the environment, wildlife and people in northern communities will help to further assess transmission risks and identify major exposure routes. Given the biological complexity of *T. gondii*, especially in an era of changing climate, understanding the ecological drivers for its persistence in northern ecosystems will be challenging. Many interesting discussions and questions remain open regarding the ecology of northern parasites, including *T. gondii* and other zoonotic pathogens. Continued collaborations between health professions and northern communities, ecologists, wildlife professionals, and natural resource experts will facilitate a multifaceted approach to northern health issues such as *T. gondii* ecology and epidemiology.

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