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SPATIOTEMPORAL DYNAMICS OF *TOXOPLASMA GONDII* INFECTION IN CANADIAN LYNX (*LYNX CANADENSIS*) IN WESTERN QUÉBEC, CANADA

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ABSTRACT: *Toxoplasma gondii*, one of the more common zoonotic parasites in the world, can cause serious illness in humans and other animals worldwide. Felids are the only known host that can shed *T. gondii* oocysts, which are essential to the perpetuation of the parasite. In much of boreal Canada, the Canadian lynx (*Lynx canadensis*) is the only wild felid host that could contribute to environmental contamination with *T. gondii* oocysts. We estimated the prevalence of *T. gondii* antibodies in Canadian lynx from western Québec and compared our results with earlier findings in the same region 12 yr earlier. We investigated factors associated with seroconversion, including age, sex, geographic location, and possible co-occurrence with domestic cats (*Felis catus*), and we assessed the proportion of lynx shedding *T. gondii* oocysts. Blood and fecal samples were collected from 84 lynx harvested by trappers in the eastern part of the study area during winter 2009–2010. Sera were tested for antibodies to *T. gondii* by the modified agglutination test (cutoff titer 1:50) and fecal samples for parasite eggs by fecal flotation. Antibodies to *T. gondii* were detected in sera of 14% of 84 lynx. Numerous helminth ova and coccidian oocysts were found in feces, whereas *T. gondii*–like oocysts were not detected. Antibody prevalence increased with age class (odds ratio [OR]=4.33, 95% confidence interval [CI]=1.57–11.99, $P<0.01$). Antibody prevalence (14%) in our study was significantly lower than in 84 lynx (36%) trapped in the western part of the study area during winter 1997–1998 (OR=0.18, 95% CI=0.08–0.44, $P<0.001$). Our results suggest there may be significant spatiotemporal dynamics of *T. gondii* infection in lynx in Canada, and we review possible abiotic and biotic ecologic factors supporting these findings.

Key words: Canadian lynx, predator-prey cycle, snowshoe hare, spatiotemporal dynamic of infection, *Toxoplasma gondii*.

INTRODUCTION

Toxoplasma gondii is a protozoan parasite with a worldwide distribution. It can cause serious illness in humans and other animals, including wildlife (Dubey, 2010). Felids are the only known definitive hosts for *T. gondii*, (i.e., the hosts in which sexual reproduction of the parasite occurs and from which oocysts are shed) (Dubey, 2010). As such they are essential to the epidemiology of this parasite. The life cycle of *T. gondii* is completed when felids ingest oocysts from the contaminated environment or tissue cysts in the infected prey.

Wild felids including lynx can shed *T. gondii* oocysts (Jewell et al., 1972; Miller et al., 1972; Jones and Dubey, 2010). Contamination of a water reservoir by oocysts shed by cougars (*Felis concolor vancouverensis*) and domestic cats (*Felis catus*) was epidemiologically linked to the largest waterborne outbreak of toxoplasmosis in humans on Vancouver Island, British Colombia, Canada (Bowie et al., 1997; Aramini et al., 1998). In much of boreal Canada, the Canadian lynx (*Lynx canadensis*) is the only wild felid and thus the only possible definitive host of *T. gondii* in sylvatic cycles. The ecology of *T. gondii* in wildlife, including the role of wild felids, has been little explored, and further study of lynx as a definitive host for this parasite in northern ecosystems is

needed (Mucker et al., 2006; Ryser-Degiorgis et al., 2006; Carme et al., 2009; Garcia-Bocanegra et al., 2010). *Toxoplasma gondii* infection in the lynx has been recently reviewed (Dubey, 2010; Jones and Dubey, 2010), and the one previous antibody prevalence study showed a relatively high *T. gondii* prevalence in the Canadian lynx from Québec, Canada (Labelle et al., 2001). Among felids, ingestion of infected tissue is the most efficient means of transmission of *T. gondii* and is likely the main source of infection of lynx (Afonso et al., 2007; Garcia-Bocanegra et al., 2010). In much of the boreal forest, therefore, the main transmission cycle is likely to involve lynx acquiring *T. gondii* infection from their prey, which, being almost entirely herbivores, would likely acquire infection by ingestion of oocysts shed by lynx. In some areas around farms and human habitations, which provide food and shelters for domestic cats (Ferreira et al., 2011; Horn et al., 2011), transmission cycles involving cats may overlap those involving lynx as sources of infective oocysts for intermediate hosts, because lynx can tolerate human presence within their home range (Mowat et al., 2000). Other known additional transmission pathways include 1) cannibalistic or carrion consumption by some predators resulting in predator-to-predator transmission, although this is likely an infrequent source of infection for lynx given that cannibalism is uncommon and they typically prefer feeding on freshly killed prey over scavenging (Mowat et al., 2000) and 2) vertical transmission by pregnant females to their offspring, although there is no evidence whether or not this occurs in Canadian lynx.

Our aims were to 1) obtain estimates of the prevalence of *T. gondii* antibodies in Canadian lynx from western Québec and compare our results with earlier findings in the same region by Labelle et al. (2001), 2) investigate factors associated with seroconversion, including age, sex, geographic location and possible co-occurrence with domestic cats that may elucidate main methods of transmission, and 3) assess the proportion of lynx shedding *T. gondii* oocysts at any one time.

MATERIALS AND METHODS

Study area and sampling

We conducted a cross-sectional study of *T. gondii* infection among trapped lynx in the Abitibi-Témiscamingue region (65,000 km^2; 48°34′N, 78°7′W), in northwestern Québec, Canada (Fig. 1). Human population density is relatively low across Abitibi-Témiscamingue (2.5 inhabitants per km^2) with urban areas and agricultural land concentrated in the western part of the region. Average precipitation is about 900 mm, which is typical of the temperate continental climate of Québec (precipitation ranging between 1,000 and 1,500 mm along the St. Lawrence Valley, and 750 and 1,000 mm in the boreal region; Statistics Canada, 2011). The temperatures are often cold, varying between −20 C and 20 C from January to June. The territory is divided into three types of trapping areas (Fig. 1): 1) traplines which are province-registered trapping areas, 2) wildlife preserves which are large protected areas intended to ensure the conservation of wildlife, and 3) the "free zone," which is land owned privately or by the Province on which there are no restrictions to trapping.

This study was based on analysis of 84 Canadian lynx collected by trappers during winter 2009–2010 (1 November–13 December) mainly from traplines, located in the northeast of Abitibi-Témiscamingue region within the Hudson Bay watershed (Fig. 1). All lynx trapped were recovered from the same fur trader. Almost all (95%) were alive when the traps were examined, and the lynx were skinned within 24 hr of killing and then immediately frozen whole at −20 C. We received the skinned carcasses in the end of trapping season, and we collected blood and fecal samples from thawed carcasses. Approximately 2 g of feces were collected from the rectum of each lynx and stored at 4 C until analysis. Blood samples were taken from the cardiac ventricles; serum obtained after centrifugation of the blood at 1,260 × G for 5 min was stored at −20 C until serologic analysis few weeks later. Lynx were classified into young (0.5 yr) and adult (≥1.5 yr) age classes according to carcass size and weight and the opening of the apical foramen of canine root as described by Quinn and Parker (1987). The

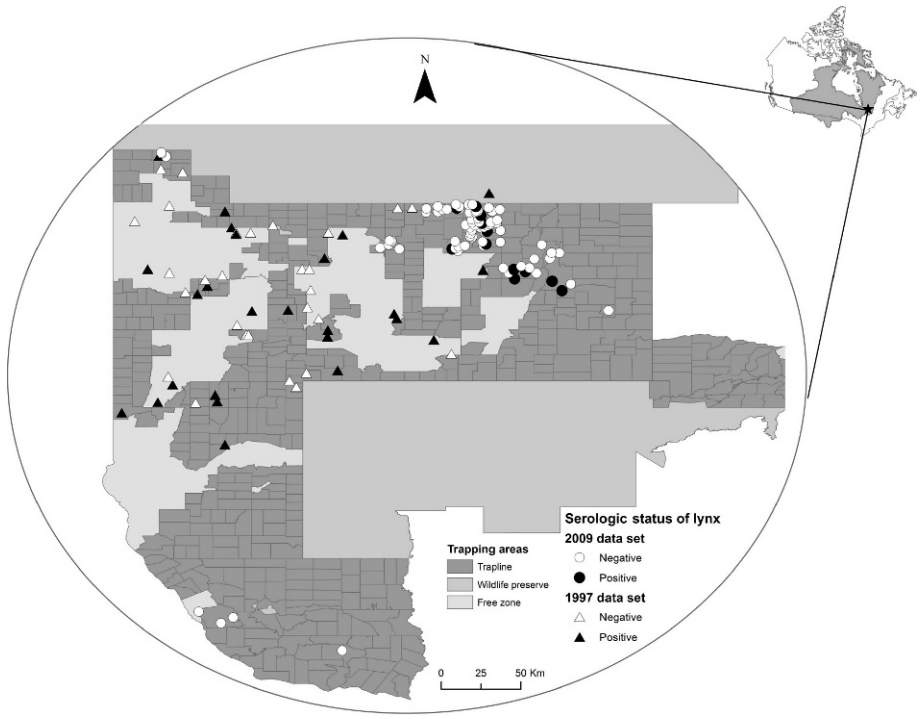

FIGURE 1. Map of the trapping area in Abitibi Témiscamingue, Québec, Canada, located in part within the Hudson Bay watershed (gray color on map of Canada in upper right) showing capture sites of Canadian lynx (*Lynx canadensis*) tested for serum antibodies against *Toxoplasma gondii*.

sex of the animals and the trapping area were recorded.

Serologic and coprologic analyses

Blood samples were tested for antibodies to *T. gondii* at the United States Department of Agriculture, Animal Parasitic Diseases Laboratory (USDA-APDL), Beltsville, Maryland, USA. Antibodies to *T. gondii* were detected by the modified direct agglutination test (MAT) as described previously by Dubey and Desmonts (1987). The MAT has been widely used to detect *T. gondii* antibodies in a variety of wild felids and is considered to be both sensitive and specific in mammals (Dubey, 2010). Positive sera were further tested at 100, 200, 400, and 800 dilutions. Positive and negative controls were included in each test. Fecal samples were examined at the Faculty of Veterinary Medicine, St-Hyacinthe, Québec, Canada, for parasite ova and protozoal oocysts by double centrifugation in a saturated zinc sulfate solution (Dryden et al., 2005). Feces were emulsified with 12 ml of tap water, then filtered through a tea strainer and centrifuged at 352 × G for 10 min. After discarding the supernatant, 10 ml of zinc sulfate solution were added until obtaining a meniscus, and the sample was again centrifuged at 352 × G for 10 min. A cover slip was placed on the surface and after 10 min transferred to a microscope slide and examined by light microscopy at 100× for evidence of parasite stages. *Toxoplasma gondii*–like oocysts were distinguishable from other coccidia based on their round shape and their diameter of 10–12 μm.

Combined analysis of our data and data from Labelle et al. (2001)

We analyzed our results with earlier findings in the same region by Labelle et al. (2001), which were based on 84 Canadian lynx recovered by trappers during the winter of 1997–1998. Prevalence of antibody to *T. gondii* with 95% confident intervals were estimated for both years and stratified by sex and age class. Additionally, spatial comparisons in antibody prevalences were made among traplines, wildlife preserves, and the "free zone" that is nearer to urbanized areas compared to traplines or wildlife preserves (MRNF, 2006). Therefore, if cats were infectious sources for lynx (via infection of intermediate hosts by

cat-derived oocysts), the lynx trapped in the "free zone" should be more exposed than the lynx trapped in the other trapping areas.

As predictors for antibody status (MAT-positive or -negative) for each lynx tested, we investigated sex, age class, year of harvesting, type of trapping area, and their first order interaction. A generalized linear model with a logit link function was used to determine whether there was significant dependence of serologic test result on the stated variables. By examining all possible combinations of predictors the most parsimonious model was selected based on a level of significance $P<0.05$ for each modeled variable (Dohoo et al., 2003). The relative goodness-of-fit of the models was assessed by Pearson and deviance chi-square tests (Dohoo et al., 2003). Statistical analyses were performed using SAS 9.1 (SAS Institute Inc., Carey, North Carolina, USA).

Additionally, to further investigate the possibility that the presence of domestic cats was a determinant of antibody status in the lynx, we explored density of farms and urban areas in the lynx home range as indicators of domesticated cat density. This possibility is relatively unlikely for the data obtained in the present study because the capture sites are a long distance from human habitation (>15 km on average), but it could have been a factor causing geographic variation in *T. gondii* antibody prevalence in the data of Labelle et al. (2001). Geographic coordinates for the 1997 dataset were available for 78 lynx, and the six missing data points were omitted from the analysis. The locations of farms in the study areas were obtained from the database of the Ministry of Agriculture, Fisheries and Food of Québec (Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec). A variable was built based on number of farms and villages or towns within a buffer representing the lynx home range and centered on each harvested lynx. Because the lynx home is highly variable across their North American range (8 to 738 km^2; Mowat et al., 2000), buffers of varying sizes were selected to conduct regression analyses (radii of 1.6, 5, 10, and 15.3 km, corresponding to a surface area of 8, 78, 314, and 735 km^2, respectively). Logistic regression models were fitted to the data for each density variable in order to explore the relationship between the serologic result for each lynx and the density of farms and cities within the lynx home range. Linearity of the relationship between the continuous variables of density and the log odds of being antibody-positive was assessed by categorizing those variables and visualizing plots of the log odds of the outcome against the midpoints of the categories (Dohoo et al., 2003). Mapping and spatial analyses were carried out using ArcMap 9.3 (ESRI Inc., Redlands, California, USA).

RESULTS

Descriptive analysis

Age–class ratios and sex ratios differed between the two sampling periods (Table 1). The sampling dataset from 1997 had larger numbers of young lynx and females compared with 2009. Antibody-positive and antibody-negative lynx were relatively well distributed across the study areas (Fig. 1). The samples used in the current study were more geographically concentrated than those used by Labelle et al. (2001), and the locations of the samplings did not overlap (Fig. 1).

In 2009, 12 of 84 lynx (14%; 95% confidence interval [CI]=7–22) were antibody-positive for *T. gondii* with serologic titers of 1:100 in eight lynx, 1:200 in three, and 1:800 in one. In comparison, 30 of 84 lynx (36%; 95% CI=25–46) were antibody-positive in 1997 at 1:50 dilution. We found numerous helminth ova and coccidian oocysts (of a size of the same order as *T. gondii* oocysts) in most fecal samples collected in 2009, whereas *T. gondii*–like oocysts were not detected. Table 1 shows the antibody prevalence among lynx according to sex, age class, and trapping area for each year of sampling. Figure 1 shows the geographic distribution and the antibody status of each sampled lynx for the two datasets.

Regression analysis

According to the most parsimonious multivariable logistic regression model for *T. gondii* antibody status, age class ($P<0.01$) and year of harvesting ($P<0.001$) were the variables kept in the model. The antibody prevalence in lynx was significantly lower in 2009 compared to 1997 (OR=0.18, 95% CI=0.08–0.44, $P<0.001$), and significantly higher in adults than young (OR=4.33, 95% CI=1.57–11.99, $P<0.01$). Sex and type of

TABLE 1. Prevalence of antibody to *Toxoplasma gondii* with 95% confident intervals (95% CI; Wald's test) in Canadian lynx trapped during the 1997 and 2009 winters in Abitibi-Témiscamingue, Québec, Canada.

	1997			2009		
Factors	No. samples	No. positive (%)	95% CI	No. samples	No. positive (%)	95% CI
Sex						
Male	30	6 (20)	6–34	55	10 (18)	8–28
Female	51	23 (45)	31–59	29	2 (7)	1–23[a]
Unknown	3	1 (33)	1–91[a]			
Age class						
Young	33	6 (18)	5–31	7	0 (0)	0–41[a]
Adult	51	24 (47)	33–61	77	12 (16)	7–24
Trapping area						
Traplines	35	14 (40)	24–58[a]	81	12 (15)	7–23
Free zone	44	13 (30)	16–43	2	0 (0)	0–84[a]
Wildlife Preserve	1	1 (100)	N/A	1	0 (0)	N/A
Unknown	4	2 (50)	7–93[a]			
Overall by year	84	30 (36)	25–46	84	12 (14)	7–22

[a] Exact 95% CI (Fisher's test).

trapping area were not significant variables in the model adjusted for potential confounding by age and sampling year ($P>0.1$). No statistically significant interaction was observed between the variables age class and year of harvesting ($P>0.1$). When the logistic regression model was recreated using data for lynx trapped in 1997, the density of farms and cities within the lynx home range were not statistically significant, regardless of the size of lynx home range used for both variables.

DISCUSSION

The antibody prevalence in lynx sampled in 2009 (14%) was lower than that found by Labelle et al. (2001; 36%) but was comparable to values found for lynx elsewhere in the world (15% to 83%; Zarnke et al., 2001; Riley et al., 2004; Jones and Dubey, 2010).

Antibody prevalence was significantly and more than fourfold (accounting for geographic/temporal variations) greater in adult than young lynx. As detectable antibody to *T. gondii* can persist for several years in many species, antibody prevalence likely represents an estimate of the cumulative likelihood of exposure for each age class (Zarnke et al., 2001; Ryser-Degiorgis et al., 2006; Garcia-Bocanegra et al., 2010). Therefore, this supports the hypothesis that the main source of *T. gondii* infection in lynx is their prey, although a low level of vertical transmission cannot be ruled out. Variation in availability of different prey species may result in variations in incidence of infection in other felid species (Kikuchi et al., 2004; Afonso et al., 2006; Ryser-Degiorgis et al., 2006), and some limited prey switching has been observed for lynx when snowshoe hare (*Lepus americanus*) population densities are low (O'Donoghue et al., 1998). However, for most years, the source of infection for the Canadian lynx is most likely snowshoe hares because lynx feed almost exclusively on this species of prey throughout their range (Mowat et al., 2000), particularly in eastern Canada where the lynx in this study were sampled (Roth et al., 2007). Evidence of infection in other species of hare has been reported in several countries (Gustafsson and Uggla, 1994; Gustafsson, Uggla, and Jarplid, 1997; Gustafsson et al., 1997; Frolich et al., 2003; Dubey, 2010; Jokelainen

et al., 2011). Although we do not have direct evidence for *T. gondii* infection in snowshoe hares in Canada, it would be expected that this species would be capable of acting as an intermediate host. As herbivores, snowshoe hares may become infected by ingestion of oocysts from contaminated herbage. Further studies on infection in snowshoe hares would help to define their role as a source of *T. gondii* infection for lynx.

In our study, antibody prevalence in lynx sampled in 2009 (14%) was significantly lower than that found during 1997 trapping (36%) accounting for increasing antibody prevalence with age. Both in our study and that of Labelle et al. (2001) sera were tested using the same methods, reagents, and serum dilutions, and so difference in antibody prevalence between the studies may be the result of spatiotemporal dynamics of *T. gondii* infection in lynx in the Canada's boreal forest. The locations of lynx trapping in 2009 and 1997 were not the same: Those trapped in 2009 were mostly from the east of the region, whereas those trapped in 1997 were mostly from the west of the region (Fig. 1), possibly because of spatial variation in trapping effort across years but also because of the trap site preferences of the trappers who provided carcasses used in the studies. Therefore, we cannot exclude a spatial effect to explain the difference in *T. gondii* antibody prevalence among lynx between the two samplings. However, the boreal forest habitat in the northern part of the Abitibi-Témiscamingue, where over 90% of lynx were trapped in both studies (Fig. 1), is homogenous across the region with the exception of variations in human densities and the presence of agricultural land, which were higher in the western compared to the eastern part of the region (MRNF, 2006). We hypothesized that this would result in higher densities of domestic cats making a greater contribution to environmental contamination with *T. gondii* oocysts in the western part of our study area (Lehrer et al., 2010; Fredebaugh et al., 2011) and greater exposure of lynx in this region via increased prevalence of infected snowshoe hare prey. However, the densities of farms and human communities within the home range of lynx trapped in the western part of Abitibi-Témiscamingue did not significantly affect the probability of a lynx being antibody-positive. Farms and urban areas, where the potential infectious contact between both felids can occur, likely represent a proxy for domestic cat density, as cats have relatively small home ranges (<5 km^2) centered on farms or urban areas (Barratt, 1997; Ferreira et al., 2011; Horn et al., 2011). It is possible that these proxy variables did not fully capture the overlap in transmission cycles maintained by lynx and domestic cats because long distance movements (>100 km) of Canadian lynx do occur (Mowat et al., 2000; Schwartz et al., 2002). To study the geographic variations in *T. gondii* transmission at a local scale, and particularly interactions with felid density, habitat, and oocyst abundance and survival, snowshoe hares that disperse shorter distances may be better sentinels (Mowat et al., 2000; Fredebaugh et al., 2011).

Temporally cyclic variations in infection prevalence could be another explanation for the higher proportion of antibody-positive lynx in 1997 than in 2009. Canadian lynx and snowshoe hares share a close relationship in their population dynamics with abundance of the lynx population varying in response to abundance of snowshoe hares (Mowat et al., 2000). This cycle has been considered as a classical predator-prey cycle (Elton and Nicholson, 1942; Krebs et al., 2001), and it is likely that parasite transmission varies depending on relative densities of intermediate and definitive hosts and variations in the birth, death, and production of susceptible, infective, and immune (if any) hosts during the cycle (Lelu et al., 2010). During periods of increasing density of lynx and hares, we would expect transmission dynamics of *T. gondii* to become

more efficient (Begon et al., 2006). Following cyclical hare crashes, the dramatic decline in lynx numbers because of lower adult and kitten survival (Mowat et al., 2000) and a lower incidence of *T. gondii* infection of hares may cause a decrease in transmission and of antibody prevalence. According to indices of lynx abundance in the Abitibi-Témiscamingue region, the lynx population was at a point of high density during the 1997 sampling period, whereas it was decreasing during the 2009 sampling period (Fortin and Tardif, 2003; Paul and Trudeau, 2010), which explains the markedly different ratio of young to adult lynx harvested in 1997 (1:1.5) compared to 2009 (1:11; Table 1). Therefore, the higher antibody prevalence in lynx in 1997 than in 2009 supports the hypothesis of lynx and hare density cycles as possible causes of variation in *T. gondii* exposure. However, abiotic factors may also explain the temporal dynamic of *T. gondii* transmission through temperature, humidity, and rainfall affecting oocyst survival (Frenkel et al., 1975; Dubey, 1998) and transmission to prey (Afonso et al., 2009).

That 14% of lynx were antibody-positive in the eastern part of Abitibi-Témiscamingue within the Hudson Bay watershed, where domestic cat density is likely very low, supports the idea that lynx may alone be capable of playing the key role of definitive host in *T. gondii* transmission cycles in wildlife. The existence of a sylvatic transmission cycle of *T. gondii* has been suggested for other wild felid species (Mucker et al., 2006; Ryser-Degiorgis et al., 2006; Carme et al., 2009; Garcia-Bocanegra et al., 2010). The Hudson Bay watershed comprises an extremely large area of boreal Canada. Therefore, oocysts potentially produced by lynx could contribute to contamination of the coastal marine environment, especially in Canada (Dubey et al., 2009; Simon et al., 2011), as those produced by domestic cats are thought to do in California (Conrad et al., 2005; Miller et al., 2008).

In our study *T. gondii* oocysts were not detected in the feces of lynx. However the difficulty in detecting *T. gondii* oocysts in felids is well recognized, and the fecal flotation method is less sensitive than mouse bioassay (Dubey, 2010) or polymerase chain reaction (PCR; Lalonde and Gajadhar, 2011), although these techniques were not available to us for this study. It is possible that low numbers of small *T. gondi*i oocysts could have been missed in our study, and it is likely that lynx, like other felids, are capable of excreting oocysts (Ryser-Degiorgis et al., 2006; Garcia-Bocanegra et al., 2010; Jones and Dubey, 2010). As some atypical genotypes of *T. gondii* do not infect mice, fecal-based PCR methods may be the method of choice for future work. Genetic characterization of circulating *T. gondii* strains in hares and lynx would also assist assessment of the relative importance of wild and domestic felids in transmission of *T. gondii* in Canada.

The lynx–snowshoe hare system may constitute a uniquely simplified natural system to study and improve our knowledge of the ecology of transmission cycles of *T. gondii* and their biotic and abiotic drivers in the wild. Immediately, the discovery of antibody-positive lynx suggests that biologists and veterinarians could acquire infection during sampling of lynx by skinning (McDonald et al., 1990) or collecting feces and should perhaps wear gloves to avoid potential contact with *T. gondii* cysts or oocysts. Additionally, in the study area, the thighs of harvested lynx are consumed by the trappers, and it would be prudent to advise trappers to cook the meat thoroughly before eating.

This study revealed that populations of Canadian lynx could be the key definitive host for *T. gondii* in the boreal forest environment, maintaining transmission by infecting their prey by environmental contamination with oocysts. Thus, lynx may be the main source of environmental contamination with *T. gondii* oocysts in

this region. However, further studies aimed at detecting oocysts in lynx feces and determining the nature of the sylvatic cycle are required to confirm this. Our study suggests that there may be spatio-temporal dynamics in the transmission cycles, which could be associated with linked cyclicity in predator and prey abundance. Further studies with additional years of data looking at *T. gondii* prevalence in relation to the predator prey cycle are required.

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