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TRANSMISSION DYNAMICS OF TOXOPLASMA GONDII IN ARCTIC FOXES (VULPES LAGOPUS): A LONG-TERM MARK-RECAPTURE SEROLOGIC STUDY AT KARRAK LAKE, NUNAVUT, CANADA

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ABSTRACT: Transmission dynamics of *Toxoplasma gondii*, a parasite of importance for wildlife and human health, are enigmatic in the Arctic tundra, where free-ranging wild and domestic felid definitive hosts are absent and rarely observed, respectively. Through a multiyear mark-recapture study (2011–17), serosurveillance was conducted to investigate transmission of *T. gondii* in Arctic foxes (*Vulpes lagopus*) in the Karrak Lake region, Nunavut, Canada. Sera from adult foxes and fox pups were tested for antibodies to *T. gondii* by using serologic methods, including the indirect fluorescent antibody test, direct agglutination test, and modified agglutination test. The overall seroprevalence was 39% in adults and 17% in pups. Mature foxes were more likely to be exposed (seroconvert) than young foxes (less than 1 yr old), with the highest level of seroprevalence in midaged foxes (2–4 yr old). Pups in two different litters were seropositive on emergence from the den, around 5 wk old, which could have been due to passive transfer of maternal antibody or vertical transmission of *T. gondii* from mother to offspring. The seropositive pups were born of seropositive mothers that were also seropositive the year before they gave birth, suggesting that vertical transmission might not be limited to litters from mothers exposed to *T. gondii* for the first time in pregnancy. All recaptured seropositive foxes remained seropositive on subsequent captures, suggesting that antibodies persist or foxes are constantly reexposed or a combination of both. The results of this study provided insights into how foxes were likely exposed to *T. gondii*, the dynamics of antibody persistence and immune response, and how the parasite was maintained in a terrestrial Arctic ecosystem in the absence of felid definitive hosts.

Key words: Arctic fox, IFAT, Karrak Lake, MAT, *Toxoplasma*, vertical transmission.

INTRODUCTION

Toxoplasma gondii is a protozoan infecting a wide taxonomic range of birds and mammals worldwide (Dubey 2010). In these warm-blooded animals, it usually causes no symptoms but can cause neurologic, ocular, and reproductive problems, especially in immunocompromised or pregnant hosts (Kim and Weiss 2008). *Toxoplasma gondii* reproduces sexually only within the intestines of felid definitive hosts, but a wide range of vertebrate intermediate hosts can be infected by ingestion of oocysts shed in feline feces (Dubey et al. 1970). Intermediate hosts can also become infected by ingestion of tissue cysts of *T. gondii* from infected prey or vertically by transmission through the placenta or by ingestion of milk from an acutely infected mother (Dubey 2009). Congenital infection occurs in wild populations of mice and in sheep and may be more common than previously thought in free-ranging wild animals (Tenter et al. 2000). In captive foxes, newborn pups with acute systemic toxoplasmosis born of experimentally infected Arctic foxes (*Vulpes lagopus*) have high mortality (Bjerkas 1990). Reports of infected vixens and

death of neonates has been demonstrated in farmed foxes (Smielewska-Los et al. 2000). Little is known about the occurrence of vertical transmission and dynamics of antibodies to *T. gondii* in wild populations of foxes, as long-term, mark-recapture studies are rare.

Even though the current world population of Arctic fox is stable at several 100,000 animals (Angerbjörn and Tannerfeldt 2014), some local populations are of conservation concern due to the effects of environmental change and competition with other carnivores, such as red foxes (*Vulpes vulpes*) moving north (Pamperin et al. 2006; Elmhagen et al. 2017). Mortality of Arctic foxes from acute disseminated *T. gondii* has occurred in Svalbard, Norway (Sørensen et al. 2005). In that population, seroprevalence was 43% in 594 foxes tested, and prevalence was higher in foxes less than 1 yr old, with seropositive foxes as young as 6–9 mo old, suggesting that vertical transmission could be an important mode of transmission in Arctic foxes (Prestrud et al. 2007), in addition to trophic interactions.

Since 2000, studies of Arctic foxes have been conducted at Karrak Lake, in Nunavut, Canada, focusing on foraging behavior and population dynamics in relation to variation in foods (Samelius et al. 2007; Samelius and Alisauskas 2017). Starting in 2011, blood from live-captured Arctic foxes was collected and analyzed for *T. gondii* annually (Elmore et al. 2016). This ongoing project is an opportunity to monitor disease transmission dynamics in a natural population of Arctic foxes. The tissue stages of *T. gondii* require invasive or postmortem techniques for detection; alternatively, serology serves as a relatively noninvasive indicator of exposure to *T. gondii*. No study has investigated seroprevalence in both mothers and pups newly emerged from their dens. Pups emerge from the den after 3–4 wk and are weaned at 6–7 wk (Audet et al. 2002).

In the rare occurrence of felid definitive hosts for *T. gondii* in the tundra regions of the Arctic, other transmission routes might occur, including vertical transmission and ingestion of tissue cysts in migratory wildlife via carnivory. Previous work has demonstrated that migratory birds are a potential source for introduction of toxoplasmosis and that adult Arctic foxes are likely infected through carnivory (Elmore et al. 2014, 2015). In this work, we examined blood samples from live-captured adults and, for the first time to our knowledge, juvenile Arctic foxes (pups), by using serologic methods for detection of antibody to *T. gondii*. This information contributed to furthering an understanding of immune responses and transmission of this ubiquitous parasite in Arctic ecosystems.

MATERIALS AND METHODS

Study area

Each spring (May–June in 2011 to 2017), adult Arctic foxes were captured at the Karrak Lake goose colony (67°14′N, 100°15′W), in the Queen Maud Gulf Bird Sanctuary, Nunavut, Canada (Fig. 1), as well as juvenile Arctic foxes (pups) in June–July in 2014–16. Over one million Ross's Geese (*Chen rossii*) and Lesser Snow Geese (*Chen caerulescens*) have nested annually at this site, making it one of the largest goose colonies on Earth (Alisauskas et al. 2012). Arctic foxes in this region rely heavily on small mammals for food (Samelius et al. 2007), including collared lemmings (*Dicrostonyx groenlandicus*), brown lemmings (*Lemmus sibiricus*), and northern red-backed voles (*Myodes rutilus*). Other food sources, such as birds and eggs, are an important part of their diet as well, especially when small mammals are scarce (Samelius et al. 2007). Nevertheless, lemming abundance remains the main factor driving fluctuation of Arctic fox population and reproduction, even when seasonally abundant foods, such as geese, are available (Samelius et al. 2011; Samelius and Alisauskas 2017).

Fox capture and blood sampling

Adult arctic foxes were captured by using box traps, a one-door live animal cage trap (Havahart model 1089, Woodstream Corporation, Lititz, Pennsylvania, USA). Traps were baited with sardines and wired open a few days prior to capture to accustom foxes to the traps. The traps were placed at locations with signs of fox activity (e.g., den sites, elevated knolls, and large rocks) in an area (5×14 km) of the central part of the goose colony. Once captured, 15 mg of tiletamine-zolazepam (Telazol®, Zoetis Inc., Kalamazoo, Michigan, USA) was injected intramuscularly into the upper part of the back leg following Samelius et al. (2003). Foxes were individually marked with

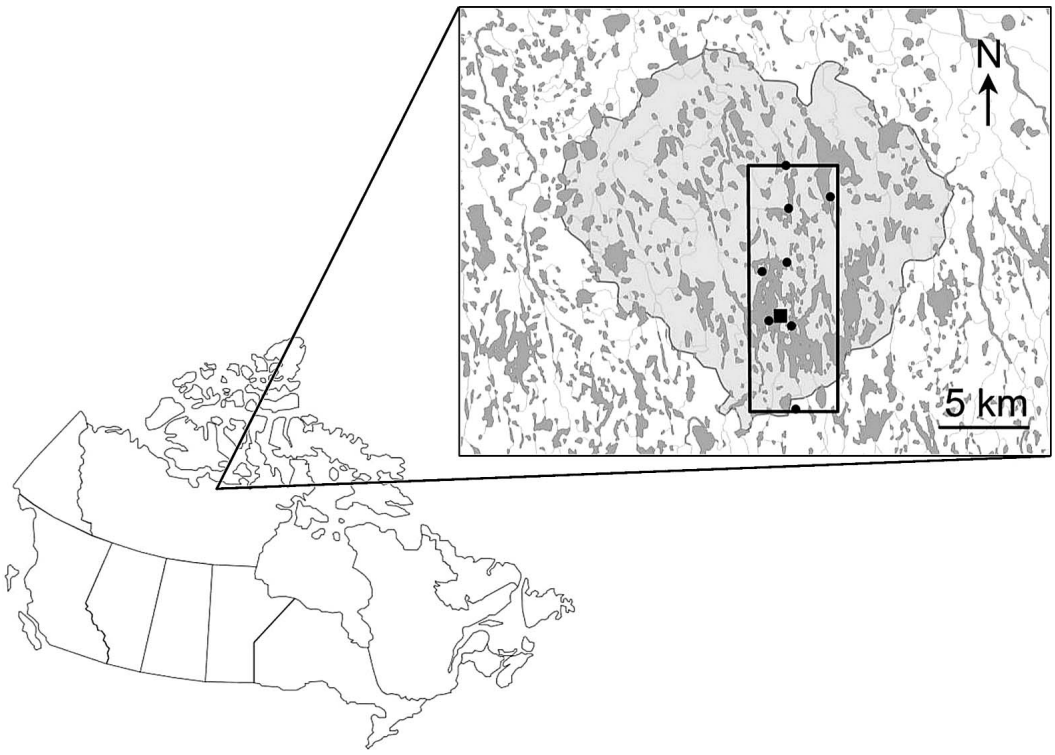

FIGURE 1. Location of the Karrak Lake Ross's Goose (*Chen rossii*) and Lesser Snow Goose (*Chen caerulescens*) colony in Nunavut, Canada, at which the transmission of *Toxoplasma gondii* in Arctic fox (*Vulpes lagopus*) was studied in a long-term (2011–17) mark-recapture serology design. The black rectangle represents the study area in the colony, the dots indicate Arctic fox dens, and the square shows the location of the field camp.

permanent plastic ear tags (1×3.5 cm in size; Dalton ID Systems Ltd., Oxfordshire, UK), weighed, and sexed. Blood samples (about 2 mL) were collected from the cephalic vein, centrifuged at 6,000 × G for 20 min, and sera stored at –20 C at the field camp for about 2 mo. Adult foxes were categorized into three different age classes on the basis of tooth wear and previous capture history following Elmore et al. (2016): young (≤1 yr old), mid aged (2–4 yr old), and older (≥5 yr old). Pups were handled as per adult foxes, except chemical immobilization was not necessary, and blood was collected from the jugular versus cephalic vein.

These procedures were approved by the University of Saskatchewan Animal Care Committee for blood collection (protocol 20100159) and live trapping (19990029) and followed the Guidelines of the Canadian Council on Animal Care. We also held wildlife research permits from the Nunavut Department of Environment (2011-018, 2012-022, 2013-017, 2014-029, 2015-019, 2016-015, and 2017-009) and Canadian Wildlife Service (NUN-MBS-11-02, NUN-SCI-11-03, NUN-MBS-14-02, and NUN-SCI-14-02).

Laboratory analysis

Each serum sample was tested by using two different serologic analyses. Samples from 2011 to 2013 were tested with a commercially available direct agglutination test (DAT) at 1:40 dilution according to the manufacturer's instructions (ToxoScreen-DA, BioMérieux, Marcy l'Etoile, France). Samples from 2014 to 2017 were tested by using a commercially available modified agglutination test (MAT) at three dilutions (1:25; 1:50; and 1:100; Al-Adhami et al. 2016) according to the manufacturer instructions (New Life Diagnostic LLC, Carlsbad, California, USA), with 1:25 as a cutoff for seropositivity. Questionable results consisting of mild agglutination covering less than half of the test well were considered negative.

In all years, an indirect fluorescent antibody test (IFAT) was performed on diluted fox serum (1:50) following the manufacturer's instructions (VMRD, Inc., Pullman, Washington, USA). Anti-

TABLE 1. Long-term trends for the presence (+) or absence (–) of antibodies to *Toxoplasma gondii* in adult Arctic foxes (*Vulpes lagopus*) recaptured at Karrak Lake, Nunavut, Canada, for 2011–17 by using the modified agglutination test and indirect fluorescent antibody test.[a]

Fox ID	Sex	Age[b]		Presence of antibodies by year[c]						
		First capture	Last capture	2011	2012	2013	2014	2015	2016	2017
OYPO	M	Mid aged	Older	–	–	–	–	–	NA	NA
PPYO	M	Mid aged	Older	–	–	NA	+	+	NA	NA
OOPP	F	Mid aged	Older	–	NA	NA	–	NA	NA	NA
OOGG	M	Older	Older	NA	+	+	NA	NA	NA	NA
PYYO	F	Young	Mid aged	NA	–	NA	+	+	NA	NA
YPPY	F	Young	Mid aged	NA	+	+	+	+	NA	NA
POPP	F	Young	Mid aged	NA	–	+	+	NA	NA	NA
PYOY	F	Young	Mid aged	NA	NA	+	+	+	NA	NA
OYYY	F	Older	Older	NA	NA	–	+	+	NA	NA
PPYY	M	Young	Mid aged	NA	NA	–	–	NA	NA	NA
YYOO	M	Mid aged	Mid aged	NA	NA	+	+	NA	NA	NA
YYGO	F	Young	Mid aged	NA	NA	–	NA	–	NA	NA
PYYY	M	Mid aged	Older	NA	NA	+	NA	+	+	NA
GOPY	F	Mid aged	Mid aged	NA	NA	NA	NA	+	+	NA
GGPP	F	Mid aged	Mid aged	NA	NA	NA	NA	NA	–	–

[a] Foxes that seroconverted are identified in boldface.

[b] Young (≤1 yr), mid aged (2–4 yr), and older (≥5 yr).

[c] NA = not taken.

canine immunoglobulin G (IgG) antibodies conjugated to fluorescein isothiocyanate (rabbit origin) were applied on slides. Slides were viewed under an Olympus BX51TF fluorescence microscope (Olympus, Tokyo, Japan), with an Olympus DP72 camera (Olympus) at 40× objective. A complete staining around the tachyzoites was considered positive for *T. gondii* antibodies. Tachyzoites with little, discontinuous, or no staining were recorded as negative.

A sample was considered positive if both the agglutination and IFAT assays gave positive results. Both tests were read by the same person for 2011–13, as well as for 2014–17, blinded between assays.

Data analysis

Statistical analyses (prevalence, mean, SE, and 95% confidence interval [CI]) were performed by using R v3.4.3 (R Development Core Team 2017). The agreements between tests were determined by the kappa (κ) coefficient, where κ=1.00 represented a perfect correlation.

RESULTS

A total of 55 individual adult foxes were captured between 2011 and 2017, with 27 recaptures (Table 1). The annual seroprevalences for *T. gondii* in adult Arctic foxes, including recaptures, were determined (Table 2). Mean seroprevalence in adults was 39% for all years of the study (SE=7, 95% CI=28–50).

In the 41 pups captured in 2014–16, the mean seroprevalence was 17% (SE=16, 95% CI=7–32), and annual seroprevalences were calculated (Table 3). For MAT, positive samples for adults and juveniles were positive at all three dilutions. The κ coefficient was 0.76 for DAT and IFAT, and 0.97 for MAT and IFAT.

Four recaptured foxes seroconverted (i.e., changed from seronegative to seropositive) over the course of the study (Table 1). By estimating the age of adults on the last capture, one was older, two were mid aged, and one was younger at the time of seroconversion. All recaptured seropositive foxes remained seropositive on subsequent captures; three foxes remained seropositive for at least 3 to 4 yr (Table 1). The age of seropositive pups ranged from 5–8 wk, all

TABLE 2. Serologic prevalence of *Toxoplasma gondii* in adult Arctic foxes (*Vulpes lagopus*), including recaptured foxes at Karrak Lake, Nunavut, Canada, for 2011–17 by using the modified agglutination test and indirect fluorescent antibody test.

Year	Sample size	No. positive (%)	95% Confidence interval
2011	10	1 (10)	0–45
2012	20	5 (25)	9–49
2013	15	8 (53)	27–79
2014	14	8 (57)	29–82
2015	14	7 (50)	23–77
2016	5	2 (40)	5–85
2017	4	1 (25)	0–81
Total	82	32 (39)	28–50

TABLE 3. Serologic prevalence of *Toxoplasma gondii* in Arctic fox (*Vulpes lagopus*) pups at Karrak Lake, Nunavut, Canada, for 2014–16 by using the modified agglutination test and indirect fluorescent antibody test.

Year	Sample size	No. positive (%)	95% Confidence interval
2014	18	1 (6)	0–27
2015	12	6 (50)	21–79
2016	11	0 (0)	0–28
Total	41	7 (17)	7–32

were still nursing when captured, and all had seropositive mothers (PYOY and PYYO) who were seropositive in previous years as well (Tables 1, 4). Three seropositive females (PYOY, POPP, and OYYY) had only seronegative pups (Table 4) at 5–9 wk old.

DISCUSSION

We demonstrated, for the first time, the presence of antibodies to *T. gondii* in free-ranging Arctic fox pups as young as 5 wk old, born of seropositive mothers. This was consistent with either passive transfer of maternal antibodies or vertical transmission of *T. gondii* from mother to young. Maternal IgG antibodies may passively transfer in utero to the fetus or through the colostrum and milk (Remington et al. 2004). Maternal antibodies represent an important part of circulating IgG in pups. The production of IgG derived from maternal antibodies usually stops abruptly as soon as weaning takes place, at around 6–7 wk of age for fox pups (Van de Perre 2003). Passive transfer may account for the single positive pup (tested at 5 wk old) of seven pups (tested at 6–9 wk old) from a seropositive female in 2014. However, antibodies were not detected in pups in the same age range (5–9 wk old) in three other litters from seropositive mothers.

For the other seropositive pups (estimated age 6–8 wk old), the entire litter demonstrated IgG antibodies against *T. gondii*, with the older pups having titers as high as the younger pups. Transfer of maternal antibodies could be a possibility, but we would expect lower detection of IgG in the older pups as the titer of IgG drops with increasing age (Omata et al. 1994). In dogs, passively transferred maternal IgG antibodies are estimated to reach their lowest point between 4 wk old and 8 wk old, depending on the intake of colostrum (Felsburg 2002). Our results provided new information about the duration of maternal antibody in free-ranging Arctic fox populations or suggested that vertical transmission of *T. gondii* might have occurred in Arctic carnivores. Vertical transmission could be either transplacental (Bresciani et al. 2009) or transmammary (Powell et al. 2001).

Interestingly, both litters with seropositive pups were from mothers that had been seropositive the year previously. If our findings did represent vertical transmission of the parasite, this suggested that transmission of *T. gondii* may occur in multiple litters. Similar findings have also been reported in deer mice (*Peromyscus maniculatus*) with *T. gondii* (Rejmanek et al. 2010) and in dogs with the closely related parasite *Neospora caninum* (Dubey et al. 1990). Previously, it was supposed that fetuses became infected with *T. gondii* only when the mammalian female was infected for the first time during pregnancy and lactation, as assumed for humans (Moncada and Montoya 2012). Finally, transmission of tachyzoites to females by males through semen also remains a possible route

TABLE 4. Serologic prevalence of *Toxoplasma gondii* in adult Arctic foxes (*Vulpes lagopus*) and their litters at Karrak Lake, Nunavut, Canada, from 2014 to 2016.[a]

Year	Fox ID	Adults		Pups tested[b]		Litter size
		Sex	Results[c]	No. positive (age)	No. negative (age)	
2014	PYOY	Female	+	1 (5 wk)	6 (5–8 wk)	7
	OYPO	Male	−	—	—	—
	POPP	Female	+	NA	6 (7–9 wk)	7
	PPYY	Male	−	—	—	—
	OYYY	Female	+	NA	5 (6–7 wk)	9
	PPYO	Male	+	—	—	—
2015	PYOY	Female	+	NA	4 (7 wk)	7
	OYPO	Male	−	—	—	—
	PPPP	Female	−	NA	2 (8 wk)	5
	Unknown	Male	NA	—	—	—
	PYYO	Female	+	6 (6–8 wk)	NA	11
	PYYY	Male	+	—	—	—
	YYYP	Female	NA	NA	NA	NA
	YYYY	Male	−	—	—	—
2016	GGOP	Female	−	NA	5 (5–8 wk)	6
	PYYY	Male	+	—	—	—
	GPGP	Female	−	NA	4 (5–8 wk)	5
	Unknown	Male	NA	—	—	—
	Unknown	Female	NA	NA	2 (7 wk)	3
	Unknown	Male	NA	—	—	—

[a] Samples from adult foxes and pups were tested by the modified agglutination test and indirect fluorescent antibody test. NA = not applicable.

[b] — = breeding male paired with the female above it.

[c] + = positive; − = negative.

for infection of female foxes and their pups (Arantes et al. 2009). However, we were unable to explore this hypothesis, as only one male mated to a seronegative female was seropositive (all of their pups were seronegative).

A significant limitation of the current study was the reliance on noninvasive sampling and serologic assays. Serology is often the only tool available for surveillance in wildlife, but results must be carefully interpreted, especially when tests optimized for domestic species or humans are used in wildlife. Agglutination (DAT or MAT) and IFAT methods were used due to their long history in wildlife surveillance for exposure to *T. gondii*, the availability of mammalian or canid-specific reagents, and their demonstrated high detection probability when compared with other test methods in Arctic fox (Elmore et al. 2016). Test results correlated well in this study, with a κ coefficient of 0.76 for DAT and IFAT and 0.97 for MAT and IFAT, showing good and very good test agreement, respectively. Finally, we were conservative in our interpretation, requiring that animals be positive for both an agglutination assay and the IFAT to be considered positive.

Live trapping, tagging, and monitoring for antibodies to *T. gondii* in adult Arctic foxes at Karrak Lake demonstrated that the overall seroprevalence was relatively stable over time (Table 2), considering the 95% CI and low sample sizes. A stable seroprevalence in the Karrak Lake fox population would indicate a constant infection pressure from their environment (Opsteegh et al. 2011), meaning that foxes are routinely exposed to *T. gondii*, whether it is by trophic or vertical transmis-

sion or both. In the long term, changes in serostatus of recaptured foxes provide insight into timing of exposure and antibody persistence in naturally infected animals. Four foxes seroconverted over the course of the study, including three mature foxes and one young fox. Mid aged and older foxes are more likely to be exposed to *T. gondii* via foodborne routes than young foxes. Three animals remained seropositive for at least 3 to 4 yr, suggesting antibody persistence or reexposure or a combination of both. Antibodies against *Toxoplasma* are usually thought to persist for a lifetime in the host, probably due to constant antigenic stimulation from persistent tissue cysts (Remington and Krahenbuhl 1982). However, a recent study highlights that lifelong persistence of tissue cysts and protective immunity to *T. gondii* has yet to be demonstrated (Rougier et al. 2017). Although our sample size of recaptured animals is not sufficient to understand fully the dynamics of antibody persistence, ongoing study of the prevalence of *T. gondii* antibodies in this fox population will provide a better idea of the dynamics of disease transmission and persistence of antibodies and whether chronic *T. gondii* infection may result in negative impacts on foxes, such as reduced reproductive success and survival.

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