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Latitudinal variability in the seroprevalence of antibodies against *Toxoplasma gondii* in non-migrant and Arctic migratory geese

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ABSTRACT

Toxoplasma gondii is an intracellular coccidian parasite found worldwide and is known to infect virtually all warm-blooded animals. It requires a cat (family Felidae) to complete its full life cycle. Despite the absence of wild felids on the Arctic archipelago of Svalbard, *T. gondii* has been found in resident predators such as the arctic fox and polar bear. It has therefore been suggested that *T. gondii* may enter this ecosystem via migratory birds. The objective of this study was to identify locations where goose populations may become infected with *T. gondii*, and to investigate the dynamics of *T. gondii* specific antibodies. Single blood samples of both adults and juveniles were collected from selected goose species (*Anser anser*, *A. brachyrhynchus*, *Branta canadensis*, *B. leucopsis*) at Arctic brood-rearing areas in Russia and on Svalbard, and temperate wintering grounds in the Netherlands and Denmark (migratory populations) as well as temperate brood-rearing grounds (the Netherlands, non-migratory populations). A modified agglutination test was used on serum, for detection of antibodies against *T. gondii*. Occasional repeated annual sampling of individual adults was performed to determine the antibody dynamics. Adults were found seropositive at all locations (Arctic and temperate, brood-rearing and wintering grounds) with low seroprevalence in brood-rearing birds on temperate grounds. As no juvenile geese were found seropositive at any brood-rearing location, but nine month old geese were found seropositive during spring migration we conclude that geese, irrespective of species and migration, encounter *T. gondii* infection in wintering areas. In re-sampled birds on Svalbard significant seroreversion was observed, with 42% of seropositive adults showing no detectable antibodies after 12 months, while the proportion of seroconversion was only 3%. Modelled variation of seroprevalence with field data on antibody longevity and parasite transmission suggests seroprevalence of a population within a range of 5.2–19.9%, in line with measured values. The high occurrence of seroreversion compared to the low occurrence of seroconversion hampers analysis of species- or site-specific patterns, but explains the absence of an increase in seroprevalence with age and the observed variation in antibody titre. These findings imply that even though infection rate is low, adults introduce *T. gondii* to the high Arctic ecosystem following infection in temperate regions.

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1. Introduction

Infectious diseases represent a significant threat to both human and animal populations. As a consequence, it is of great relevance to understand the infection dynamics and distribution of important zoonotic pathogens (Altizer et al., 2011). *Toxoplasma gondii* is a globally distributed coccidian protozoan (Dubey, 2010). Infection with *T. gondii* is one of the most common parasitic infections of warm-blooded animals worldwide, including humans (Dubey and Beattie, 1988; Tenter et al., 2000). A wide range of mammals and birds can serve as intermediate hosts, where asexual reproduction and tissue cyst formation occur. Intermediate hosts can be infected by ingestion of oocysts or tissue cysts, and in some cases by placental transmission. Sexual reproduction can only happen in the intestines of the definitive host and results in infective oocysts being shed with their faeces. Oocysts are essential for the transmission to a non-carnivorous host and are only shed by domestic cats and other felines (Dubey, 2010). As the cat population has developed parallel to the human population, there is a strong potential for *T. gondii* transmission in rural settings (Amendoeira et al., 2003). Oocysts have been found both in water and in soil samples around human dwellings (Weigel et al., 1999; Dubey, 2010) and may enter the marine environment through freshwater runoff or via sewage systems (Lindsay et al., 2003; Conrad et al., 2005). Here, the oocysts can travel long distances via physical and biological processes, the latter including ingestion by marine mammals or accumulation in filter feeding fish and bivalves (Arktush et al., 2003; Fayer et al., 2004; Miller et al., 2008; Massie et al., 2010).

Polar regions are isolated both by their extreme environment and remote position. Nevertheless, both in Arctic (Prestrud et al., 2007; Oksanen et al., 2009; Jensen et al., 2010) and sub-Antarctic (Afonso et al., 2007) regions individuals seropositive with *T. gondii* have been found. Clearly, *T. gondii* is found in areas not inhabited by its definitive host. For example, in the high Arctic Svalbard archipelago (78–81°N, 10–30°E), including the main island Spitsbergen, no wild felines are present and domestic cats are prohibited. Yet, *T. gondii* infection has been observed in resident top predators such as Arctic foxes (*Vulpes lagopus*) and Polar bears (*Ursus maritimus*) (Prestrud et al., 2007). Whether the initial infection is a result of oocysts transported via ocean currents or tissue cysts from migratory animals is unknown.

Ecosystems are connected via seasonal migrations (reviewed in Altizer et al., 2011). Along the flyway migratory birds may transport infectious disease agents (Bradley et al., 2005; Altizer et al., 2011) and Prestrud et al. (2007, 2008a, 2008b) suggested that *T. gondii* is brought to the Arctic by migratory birds. In support of this notion, 7% of migratory barnacle geese (*Branta leucopsis*) on Svalbard were found seropositive, whereas no resident herbivores such as Svalbard reindeer (*Rangifer tarandus platyrhynchus*) ($n = 390$) or sibling voles (*Microtus epiroticus*) ($n = 361$) were found seropositive, suggesting that *T. gondii* oocysts in the terrestrial ecosystem are not an important mode of transmission on Svalbard (Prestrud et al., 2007). In the same study, foxes captured at sites devoid of goose colonies showed lower seroprevalence than foxes captured close to goose colonies (Prestrud et al., 2007). In addition, as the Svalbard goose populations have doubled over the last decades (Fox et al., 2010), so has the prevalence of antibodies to *T. gondii* in Svalbard's polar bears (Oksanen et al., 2009; Jensen et al., 2010).

The objective of this study was to determine *T. gondii* seroprevalence in goose populations at various locations in order to assess the role of migratory birds as vector of *T. gondii* to isolated Arctic ecosystems. As juveniles are infection naïve at birth and limited in their habitat exposure, they were specifically targeted to determine the area of infection. To this end, we sampled adults and juveniles of two arctic migratory goose species; the barnacle goose (*Branta leucopsis*) and the pink-footed goose (*Anser brachyrhynchus*), at Arctic breeding and temperate wintering grounds. To expand the sampling of the temperate environment, resident Dutch populations of barnacle, Canada (*B. canadensis*) and greylag geese (*A. anser*) were included, sampled during the brood-rearing period.

Our main assumption was that the likelihood of infection with *T. gondii* is high in areas with suspected high densities of cats, and that infection results in increased specific antibody levels in the blood. Both adult and juvenile geese would consequently show higher seroprevalence at temperate, compared to Arctic, locations. Therefore, the following hypotheses were tested: (i) in arctic areas only adults are seropositive; (ii) in temperate areas both adults and juveniles are seropositive, and both show a higher titre of antibodies in the blood: (iii) the proportion of seropositive individuals increases with age.

2. Materials and methods

Blood samples were collected between 2006 and 2010 at four locations: Svalbard (1), Nenets Autonomous Okrug NW Russia (2), Denmark (3) and the Netherlands (4) (Fig. 1). In the Arctic, birds were sampled on Spitsbergen, the western island of Svalbard (79°N/12°E) and in NW Russia at Tobseda (68°N/52°E) and Kolguev (69°N/49°E). In Denmark all birds were sampled during spring staging at Vest Stadil Fjord (58°N/8°E). In the Netherlands birds were sampled in the provinces of Groningen, Friesland, Gelderland, Noord and Zuid Holland (52°N/4°E – 53°N/6°E) during summer and in Friesland (53°N/6°E) during winter staging (Table 1).

In total four species of wild geese were investigated: barnacle goose ($n = 1543$), pink-footed goose ($n = 787$), greylag goose ($n = 266$) and Canada goose ($n = 79$) (Table 1). In the Arctic, barnacle geese were sampled from populations using two different flyways; those migrating from Arctic Russia to the Netherlands and those migrating from Svalbard to Scotland (Black et al., 2007). A second species sampled in the Arctic was the pink-footed goose migrating from Svalbard to Denmark–the Netherlands–Belgium (Madsen et al., 1999). The pink-footed goose is sharing habitat with both the earlier mentioned migratory barnacle goose populations. The migratory and non-migratory populations have overlapping winter habitats though do not fully mix during winter staging (van der Jeugd et al., 2001).

Both juvenile and adult birds were sampled at all locations (Table 1). Juvenile birds caught in Denmark were a