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Serosurvey for *Toxoplasma gondii* in arctic foxes and possible sources of infection in the high Arctic of Svalbard

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Abstract

Samples (blood or tissue fluid) from 594 arctic foxes (*Alopex lagopus*), 390 Svalbard reindeer (*Rangifer tarandus platyrhynchus*), 361 sibling voles (*Microtus rossiaemeridionalis*), 17 walruses (*Odobenus rosmarus*), 149 barnacle geese (*Branta leucopsis*), 58 kittiwakes (*Rissa tridactyla*), and 27 glaucous gulls (*Larus hyperboreus*) from Svalbard and nearby waters were assayed for antibodies against *Toxoplasma gondii* using a direct agglutination test. The proportion of seropositive animals was 43% in arctic foxes, 7% in barnacle geese, and 6% (1 of 17) in walruses. There were no seropositive Svalbard reindeer, sibling voles, glaucous gulls, or kittiwakes. The prevalence in the arctic fox was relatively high compared to previous reports from canid populations. There are no wild felids in Svalbard and domestic cats are prohibited, and the absence of antibodies against *T. gondii* among the herbivorous Svalbard reindeer and voles indicates that transmission of the parasite by oocysts is not likely to be an important mechanism in the Svalbard ecosystem. Our results suggest that migratory birds, such as the barnacle goose, may be the most important vectors bringing the parasite to Svalbard. In addition to transmission through infected prey and carrion, the age-seroprevalence profile in the fox population suggests that their infection levels are enhanced by vertical transmission.

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Keywords: *Alopex lagopus*; *Branta leucopsis*; *Larus hyperboreus*; *Microtus rossiaemeridionalis*; *Odobenus rosmarus*; *Rangifer tarandus*; *Rissa tridactyla*; Svalbard; *Toxoplasma gondii*

1. Introduction

Toxoplasma gondii is a coccidian protozoan of the phylum Apicomplexa that has a global distribution.

Definitive hosts are the domestic cat (*Felis catus*) and other felids, which harbour the sexual stages of the parasite in the intestines and shed infective oocysts with their faeces (Frenkel et al., 1970). A wide range of mammals and birds can serve as intermediate hosts, in which asexual reproduction and tissue cyst formation occur (Dubey and Beattie, 1988). Intermediate hosts can be infected by ingestion of oocysts

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or tissue cysts, or via vertical transmission (Dubey and Beattie, 1988).

Svalbard is a high arctic archipelago (78–81°N, 10–30°E) located midway between the Norwegian mainland and the North Pole. No wild felids are present on Svalbard, and domestic cats are prohibited. Nevertheless, some cats are found in the mining settlement Barentsburg. The arctic fox (*Alopex lagopus*) is a top predator, preying on birds and seal pups, and scavenging on any food item available (Eide et al., 2005). This also includes cannibalism (Prestrud, 1992). The polar bear (*Ursus maritimus*) is the top of the marine food chain. The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is widespread, whereas the sibling vole (*Microtus rossiaemeridionalis*) has a very restricted distribution around the former mining station at Grumant (78°11'N, 15°09'E) (Henttonen et al., 2001). The glaucous gull (*Larus hyperboreus*) is an avian top predator and scavenger, and is top of its food chain in the Arctic. All bird species on Svalbard, except the Svalbard rock ptarmigan (*Lagopus muta hyperborea*), are migratory, leaving the islands in the autumn (Strøm, 2006).

Three arctic foxes found dead on Svalbard in 2000 had disseminated toxoplasmosis (Sørensen et al., 2005), suggesting a possible role for *T. gondii* as a mortality factor in this species. In the present study, we analysed a large number of arctic fox samples from Svalbard for antibodies against *T. gondii*, and looked for evidence of negative effects of *T. gondii* infection on the physical condition of the hosts. We also analysed samples from several other species to evaluate the most likely transmission routes of *T. gondii* in this arctic ecosystem. Even though felids are nearly non-existent in the ecosystem, we evaluated the potential for oocyst transmission using terrestrial herbivores, the sibling vole and Svalbard reindeer, as indicators. We evaluated the potential importance of migratory birds as a source of infection by testing barnacle geese (*Branta leucopsis*), and tested walruses (*Odobenus rosmarus*), glaucous gulls, and kittiwakes (*Rissa tridactyla*) to obtain information on the potential occurrence of *T. gondii* in

the marine food chain. We also fitted simple models of the transmission dynamics of *T. gondii* to data from the fox population to evaluate the potential importance of vertical transmission.

2. Materials and methods

2.1. Animals and samples

The samples of blood (serum or plasma) and tissue fluids included in this study were from arctic foxes ($n = 594$), Svalbard reindeer ($n = 390$), sibling voles ($n = 361$), walruses ($n = 17$), kittiwakes ($n = 58$), barnacle geese ($n = 149$), and glaucous gulls ($n = 27$) from Svalbard. All live animals sampled for this study were cared for in accordance with the current regulations of the Norwegian Animal Welfare Act, and with the permission of the Norwegian Animal Research Authority and the Governor of Svalbard.

2.2. Arctic fox

Foxes were caught by fur trappers using baited traps between 1 November and 15 March 1996–1997 ($n = 11$), 1997–1998 ($n = 103$), 1998–1999 ($n = 107$), 1999–2000 ($n = 74$), 2000–2001 ($n = 25$), 2001–2002 ($n = 116$), 2002–2003 ($n = 84$), and 2003–2004 ($n = 74$). Following trapping, the carcasses were usually stored outdoors under varying conditions, exposed to freezing and thawing, which often resulted in poor carcass quality. The zoonotic cestode *Echinococcus multilocularis* is present within the Svalbard fox population (Henttonen et al., 2001), and to kill the eggs of this parasite, the carcasses were frozen at $-80\text{ }^{\circ}\text{C}$ for a minimum of 7 days (Veit et al., 1995). Later storage was at $-20\text{ }^{\circ}\text{C}$ until necropsy, when blood and tissue fluids were collected from the heart chambers, larger vessels, or thoracic cavity. After centrifugation ($1000 \times g$, 10 min), the supernatant was collected and stored at $-20\text{ }^{\circ}\text{C}$ for later analysis, and all samples, which were usually extensively haemolysed,

Table 1

Proportion (%) of *Toxoplasma gondii* seropositive arctic foxes (with 95% CI) by age group and geographic area

Age group (years)	<i>n</i>	Nordenskiöld Land, East of Isfjorden, Kapp Wijk, Farmhamna, Kongsfjorden, and Mushamna	<i>n</i>	Austfjordnes
<1	215	43 (36–49)	42	17 (8–31)
1	102	36 (28–46)	9	56 (27–81)
2	40	60 (44–74)	8	13 (1–47)
≥3	66	67 (55–77)	9	56 (27–81)

n = sample size.

were centrifuged again immediately before analysis to remove interfering precipitates.

The ages of 491 foxes were determined by counting the annuli in the cementum of a sectioned canine tooth (Grue and Jensen, 1976). Mean age was 2.1 ± 1.9 years, and the oldest fox was a 13-year-old female. The foxes were grouped by age as: <1-year old, 1-year old, 2 years old, and ≥ 3 years old (Table 1). A fat index was determined for 579 foxes by visual inspection of the amount of body fat on the skinned carcasses, on a scale from 0 (none) to 4 (extensive) (Prestrud and Nilssen, 1992).

Foxes with a known capture site ($n = 574$) were grouped according to trapping area (Fig. 1). The groupings used were (1) Nordenskiöld Land Peninsula, (2) the east end of Isfjorden, (3) Kapp Wijk, (4) Farmhamna, (5) Kongsfjorden, (6) Austfjordnes, and (7) Mushamna.

2.3. Svalbard reindeer

The reindeer were captured on Nordenskiöld Land in April or May of 2000, 2003, 2004, and 2005. Of the 390 reindeer captured, 157 (40.3%) were recaptured in one or



Fig. 1. Map showing sampling locations on Svalbard of arctic fox (1–7), barnacle goose (5), Svalbard reindeer (1), sibling vole (8), walrus (9), kittiwake (5), and glaucous gull (8 and Bjørnøya): 1, Nordenskiöld Land; 2, East of Isfjorden; 3, Kapp Wijk; 4, Farmhamna; 5, Kongsfjorden; 6, Austfjordnes; 7, Mushamna; 8, Grumant; 9, East Coast.

more subsequent years, resulting in 612 samples in total. The reindeer were grouped into age classes—calves, yearlings, and adults; 62% of the animals were adults at the time of their last capture. The reindeer were caught using a net thrown from a snow scooter and were manually restrained for sampling. Blood was drawn from the jugular vein into evacuated heparinised tubes. Plasma was collected after centrifugation and frozen. Each animal was ear tagged at the time of the first capture.

2.4. Sibling vole

The voles were captured during summers and autumns of 2002–2005 in the Grumant area (Fig. 1), the only vole habitat on Svalbard. The area has a high density of arctic foxes and several of the foxes trapped on Nordenskiöld Land Peninsula were trapped in Grumant and nearby sites (Longyearbyen, Bjørndalen and Colesdalen). The voles were live captured in baited traps and bled from the tail tip (Microvette CB 300 capillary tubes, Sarstedt, Nürnberg, Germany), or killed in snap traps (blood was drawn from the heart or thoracic cavity). Serum was collected and stored at $-20\text{ }^{\circ}\text{C}$.

2.5. Walrus

Seventeen adult male walruses were captured at different locations on the east coast of Svalbard (Fig. 1) in August 2002–2004. They were immobilized with etorphine, which was reversed with diprenorphine after sampling (Griffiths et al., 1993). Blood was drawn from the extradural vertebral vein, and serum was stored at $-20\text{ }^{\circ}\text{C}$.

2.6. Bird species

Adult kittiwakes were caught on their nests in Kongsfjorden (Fig. 1) in 2005, using a telescopic fishing rod with a noose at the end. The glaucous gulls were found dead during the period 2003–2005 on Bjørnøya (Fig. 1; $n = 25$), the southernmost island of Svalbard, and in the Grumant area ($n = 2$). Blood was collected from the heart during necropsy, and the serum was stored frozen. The barnacle geese were all adults, captured while flocks of geese were ringed in the Ny-Ålesund area (Fig. 1) in Kongsfjorden in 2005. Blood from kittiwakes and geese was drawn from the brachial vein.

2.7. Direct agglutination test (DAT)

Samples were assayed for antibodies to *T. gondii* at 1:40 dilutions, using the Toxo-Screen DA kit

(bioMérieux S.A., Marcy-l'Etoile, France) according to the manufacturer's instructions. Samples that became agglutinated at this dilution were defined as seropositive and were assayed further at dilutions of 1:160, 1:640, and 1:1280.

2.8. Statistical analyses

The frequency of *T. gondii*-positive samples was analysed using logistic regression. We also estimated the age-specific infection rates of *T. gondii* infections, following the method outlined by Ades and Nokes (1993), using the catalytic infection model:

$$q(a_c) = \exp \left[- \int_0^{a_c} \lambda(a) da \right]$$

where $q(a_c)$ is the fraction of individuals of age a_c that are seronegative for *T. gondii* and $\lambda(a)$ is the age-specific force of *T. gondii* infection with constraint $\lambda(a) \geq 0$. This model assumes that: (1) individuals can become infected only once and stay seropositive thereafter for the rest of their lives; (2) the host population size stays constant and there is no migration; (3) host death due to infection is negligible; (4) the population of individuals of age a_c is homogeneous with respect to susceptibility and exposure to infection; and (5) the importance of maternally derived passive immunity is negligible and therefore all animals are born either infected by vertical transmission or susceptible (Nokes, 1993). Score-test-based confidence limits were calculated for simple proportions (Agresti and Coull, 1998), whereas likelihood ratio-based confidence limits were calculated for model parameters.

3. Results

The proportion of *T. gondii* seropositive arctic foxes was 43%. Among the other species investigated, only barnacle geese and one walrus were seropositive for *T. gondii* (Table 2). Titres were generally high in positive samples; a goose, the positive walrus, and 58% of the seropositive foxes had titres of $\geq 1:1280$.

Among the foxes, the proportion of seropositive individuals increased significantly with age, both when analysed as a continuous variable (0–13 years; $P < 0.0001$) and when categorical age groups were used ($P = 0.0002$). There was also evidence of an additive variation in proportions of seropositive individuals between sampling locations ($P = 0.01$). However, there were no significant differences in prevalence between the sexes ($P = 0.84$), between years

Table 2

The number of individuals tested (n), number of seropositive individuals (no. of positive), and percent seropositive animals, with 95% CI, for each of the species investigated

Species	n	No. of positive	Seropositive (%)	95% CI
Arctic fox	594	257	43	39–47
Barnacle goose	149	11	7	4.2–12.7
Svalbard reindeer	390	0	0	0–1
Sibling vole	361	0	0	0–1.1
Walrus	17	1	6	0.3–27
Kittiwake	58	0	0	0–6.2
Glaucous gull	27	0	0	0–12.5

of capture ($P = 0.18$), or any interaction between these predictor variables ($P > 0.10$). In addition, there was no evidence for a relationship between the fat index of the foxes and their *T. gondii* serological status ($P = 0.65$).

The spatial variation in the proportion of seropositive foxes was mainly due to a lower proportion at Austfjordnes compared to the other locations ($P = 0.001$, Table 1), with no significant variation between the other locations ($P = 0.27$). The variation in proportion of positive individuals with age was fairly erratic at Austfjordnes, possibly due to small sample sizes from this location (Table 1). At the other locations, the first two age groups (<1- and 1-year-old foxes) showed similar seroprevalences, with a tendency towards a reduction from the first to the second year of life, and then a marked increase in prevalence in 2- and ≥ 3 -year-old groups (Table 1).

When fitting the catalytic infection model to the data, we excluded the data from Austfjordnes because it showed a pattern very different from the other locations. The estimates of force of infection (λ) suggested high rates of infection in the <1-year-old group ($\lambda = 0.53$; 95% CI: 0.44–0.62), no new infections in the 1-year-old group ($\lambda = 0.00$; 95% CI: 0.00–0.13), and an intermediate rate of infection in the 2- and ≥ 3 -year-old groups ($\lambda = 0.18$; 95% CI: 0.12–0.42). There was no significant difference in force of infection between 2- and ≥ 3 -year-old groups ($P = 0.40$). The force of infection was significantly higher in <1-year-old group than in ≥ 2 -year-old groups ($P < 0.0001$).

4. Discussion

The proportion of foxes with antibodies against *T. gondii* among the 594 individuals assayed was 43%. In a study on red foxes (*Vulpes vulpes*) from Hungary, the proportion with antibodies against *T. gondii* was 68% (Jakubek et al., 2007), whereas in red foxes from other European countries seropositive proportions of 20–38%

have been demonstrated (Kapperud, 1978; Jakubek et al., 2001; Hamilton et al., 2005; Wanha et al., 2005). The occurrence of *T. gondii* in arctic foxes from Svalbard is thus very high, and there is reason to believe that the true seroprevalence may have been underestimated as a result of the poor quality of many samples. Degraded sample material is shown to be valuable for use in serological assays, but may lead to under-estimation of true prevalences (Tryland et al., 2006). Tissue fluid is reported to be a good alternative to blood samples for serological assays (Gamble and Patrascu, 1996; Tryland et al., 2006).

Svalbard reindeer are the main mammalian herbivore on the islands, and could be expected to pick up oocysts from the ground if they were present. Previous reports have suggested oocysts as a likely source of transmission of *T. gondii* to semi-domesticated reindeer (*Rangifer tarandus tarandus*) in Fennoscandia (Oksanen et al., 1997) and barren-ground caribou (*Rangifer tarandus groenlandicus*) in Canada (Kutz et al., 2001). The finding of no seropositive reindeer or sibling voles indicates that infection by oocysts is not an important mode of transmission on Svalbard.

The finding of 7% seropositive barnacle geese shows that a significant proportion of barnacle geese migrating to Svalbard harbours *T. gondii*. This suggests that barnacle geese, and possibly other migratory birds, may function as an important source of *T. gondii* to the ecosystem. Barnacle geese breeding on Svalbard may become infected by oocysts from cat faeces in their winter habitat on agricultural land in southern Scotland (Owen and Gullestad, 1984), or during their migration along the Norwegian coast. The barnacle goose is common throughout Svalbard (population size estimated to be 27,000 in 2005; Strøm, 2006), and it is known to be an important prey species to the arctic fox (Jepsen et al., 2002; Fuglei et al., 2003; Eide et al., 2005). The low proportion of seropositive foxes at Austfjordnes supports the idea that migratory geese are an important source of infection, since this was the only sample site with no barnacle goose colonies nearby (Mehlum, 1998; SCRIB, 2007).

One seropositive walrus was identified, showing that *T. gondii* is present in the marine food chain. Walrus mainly feed on marine invertebrates, but some also eat seals, and cannibalism has been reported (Lowry and Fay, 1984; review by Forbes, 2000; Born et al., 2003). It has also been proposed, but never actually shown, that walrus scavenge on polar bear carcasses (Larsen and Kjos-Hansen, 1983; review by Forbes, 2000). In support of a marine source of infection, Oksanen et al. (unpublished results) have found antibodies against

T. gondii among polar bears around Svalbard. However, even though high seroprevalences of *T. gondii* have been found in various seal species from Alaska and Northern Canada (Dubey et al., 2003; Measures et al., 2004), previously studied marine mammals (harp seals, *Phoca groenlandica*; ringed seals, *Pusa hispida*; hooded seals, *Cystophora cristata*; and minke whales, *Balaenoptera acutorostrata*) from the Northern Atlantic Ocean were all found to be seronegative (Oksanen et al., 1998). This may indicate that *T. gondii* is not very prevalent in the marine ecosystem around Svalbard, a hypothesis also supported by the seronegative kittiwakes and glaucous gulls. Nevertheless, we cannot reject the possibility that walruses, foxes and polar bears from time to time might become infected through seal prey or seal carrion. Disease transmission via invertebrate prey to marine mammals has been suspected in previous reports; either from filter feeding molluscs, as reported for *T. gondii* (Miller et al., 2002), or through transport of undigested pieces of scavenged flesh, as reported for *Trichinella* (reviewed by Forbes, 2000). We cannot exclude the possibility that transmission from human activities to terrestrial or marine animals might also occur. Meat scraps may occasionally be available, although garbage regulations are strict.

Among the foxes, the force of infection was higher in <1-year-old group than in other groups. Maternal antibodies against rabies virus in the red fox are reported to have a half-life of 8–10 days (Müller et al., 2002). The youngest foxes assayed were 6–9-month-old; and thus it is unlikely that the high seropositive proportion in the youngest age group was caused by maternal antibodies. This indicates that vertical transmission may be important in the arctic fox. Vertical transmission is shown to occur in experimentally infected farmed arctic foxes and spontaneously in numerous other species, and generally occurs when the mother suffers primary infection during pregnancy (Dubey and Beattie, 1988; Bjerkås, 1990; Duncanson et al., 2001; Marshall et al., 2004). Parasite-induced host mortality would also affect estimates of force of infection, and may be common even though we found no evidence for chronic effects of *T. gondii* infection on the physical condition of the foxes as measured by the fat index.

In conclusion, we suggest that *T. gondii* most likely is brought to Svalbard by migratory birds that become infected in temperate agricultural areas in the winter. However, marine sources of infection may exist. The high seroprevalence of *T. gondii* in the arctic fox population on Svalbard may be due to: (1) infection from migratory bird species through predation; (2)

vertical transmission; and (3) tissue cyst transmission within the Svalbard ecosystem through scavenging and cannibalism. Together, these transmission routes cause a surprisingly high seroprevalence of *T. gondii* in a top predator living in an ecosystem with very few cats.

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References

- Ades, A.E., Nokes, D.J., 1993. Modeling age- and time-specific incidence from seroprevalence: toxoplasmosis. *Am. J. Epidemiol.* 137, 1022–1034.
- Agresti, A., Coull, B.A., 1998. Approximate is better than “exact” for interval estimation of binomial proportions. *Am. Stat.* 52, 119–126.
- Bjerkås, I., 1990. Neuropathology and host–parasite relationship of acute experimental toxoplasmosis of the blue fox (*Alopex lagopus*). *Vet. Pathol.* 27, 381–390.
- Born, E.W., Rysgaard, S., Ehlme, G., Sejr, M., Acquarone, M., Levermann, N., 2003. Underwater observations of foraging free-living Atlantic walruses *Odobenus rosmarus rosmarus* and estimates of their food consumption. *Polar Biol.* 26, 348–357.
- Dubey, J.P., Beattie, C.P., 1988. *Toxoplasmosis of Animals and Man*. CRC Press, Boca Raton, Florida.
- Dubey, J.P., Zarnke, R., Thomas, N.J., Wong, S.K., Van Bonn, W., Briggs, M., Davis, J.W., Ewing, R., Mense, M., Kwok, O.C.K., Romand, S., Thulliez, P., 2003. *Toxoplasma gondii*, *Neospora caninum*, *Sarcocystis neurona* and *Sarcocystis canis*-like infections in marine mammals. *Vet. Parasitol.* 116, 275–296.
- Duncanson, P., Terry, R.S., Smith, J.E., Hide, G., 2001. High levels of congenital transmission of *Toxoplasma gondii* in a commercial sheep flock. *Int. J. Parasitol.* 31, 1699–1703.
- Eide, N.E., Eid, P.M., Prestrud, P., Swenson, J.E., 2005. Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape. *Wildl. Biol.* 11, 109–121.
- Forbes, L.B., 2000. The occurrence and ecology of *Trichinella* in marine mammals. *Vet. Parasitol.* 93, 321–334.
- Frenkel, J.K., Dubey, J.P., Miller, N.L., 1970. *Toxoplasma gondii* in cats: fecal stages identified as coccidian oocysts. *Science* 167, 893.
- Fuglei, E., Øritsland, N.A., Prestrud, P., 2003. Local variation in arctic fox abundance on Svalbard, Norway. *Polar Biol.* 26, 93–98.
- Gamble, H.R., Patrascu, I.V., 1996. Whole blood, serum and tissue fluids in an enzyme immunoassay for swine trichinellosis. *J. Food Prot.* 59, 1213–1217.
- Griffiths, D., Wiig, Ø., Gjert, I., 1993. Immobilization of walrus with etorphine hydrochloride and Zoletil®. *Mar. Mamm. Sic.* 9, 250–257.

- Grue, H., Jensen, B., 1976. Annual cementum structures in canine teeth in arctic foxes (*Alopex lagopus* L.) from Greenland and Denmark. *Danish Rev. Game Biol.* 10, 1–12.
- Hamilton, C.M., Gray, R., Wright, S.E., Gangadharan, B., Laurenson, K., Innes, E.A., 2005. Prevalence of antibodies to *Toxoplasma gondii* and *Neospora caninum* in red foxes (*Vulpes vulpes*) from around the UK. *Vet. Parasitol.* 130, 169–173.
- Henttonen, H., Fuglei, E., Gower, C.N., Haukisalme, V., Ims, R.A., Niemimaa, J., Yoccoz, N.G., 2001. *Echinococcus multilocularis* on Svalbard: introduction of an intermediate host has enabled the local life-cycle. *Parasitology* 123, 547–552.
- Jakubek, E.-B., Brøjer, C., Regnersen, C., Uggla, A., Schares, G., Björkman, C., 2001. Seroprevalences of *Toxoplasma gondii* and *Neospora caninum* in Swedish red foxes (*Vulpes vulpes*). *Vet. Parasitol.* 102, 167–172.
- Jakubek, E.-B., Farkas, R., Pálfi, V., Mattsson, J.G., 2007. Prevalence of antibodies against *Toxoplasma gondii* and *Neospora caninum* in Hungarian red foxes (*Vulpes vulpes*). *Vet. Parasitol.* 144, 39–44.
- Jepsen, J.U., Eide, N.E., Prestrud, P., Jacobsen, L.B., 2002. The importance of prey distribution in habitat use by arctic foxes (*Alopex lagopus*). *Can. J. Zool.* 80, 418–429.
- Kapperud, G., 1978. Survey for toxoplasmosis in wild and domestic animals from Norway and Sweden. *J. Wildl. Dis.* 14, 157–162.
- Kutz, S.J., Elkin, B.T., Panayi, D., Dubey, J.P., 2001. Prevalence of *Toxoplasma gondii* antibodies in barren-ground caribou (*Rangifer tarandus groenlandicus*) from the Canadian Arctic. *J. Parasitol.* 87, 439–442.
- Larsen, T., Kjos-Hansen, B., 1983. *Trichinella* sp. in polar bears from Svalbard, in relation to hide length and age. *Polar Res.* 1, 89–96.
- Lowry, L.F., Fay, F.H., 1984. Seal eating walrus in the Bering and Chukchi seas. *Polar Biol.* 3, 11–18.
- Marshall, P.A., Hughes, J.M., Williams, R.H., Smith, J.E., Murphy, R.G., 2004. Detection of high levels of congenital transmission of *Toxoplasma gondii* in natural urban populations of *Mus domesticus*. *Parasitology* 128, 39–42.
- Measures, L.N., Dubey, J.P., Labelle, P., Martineau, D., 2004. Seroprevalence of *Toxoplasma gondii* in Canadian pinnipeds. *J. Wildl. Dis.* 40, 294–300.
- Mehlum, F., 1998. Areas in Svalbard important for geese during the pre-breeding, breeding and post-breeding periods. In: Mehlum, F., Black, J.M., Madsen, J. (Eds.), *Research on Arctic geese. Proceedings of the Svalbard Goose Symposium Norsk Polarinstittutt Skrifter* 200, Oslo, Norway, September 23–26 1997, pp. 41–55.
- Miller, M.A., Gardner, I.A., Kreuder, C., Paradies, D.M., Worcester, K.R., Jessup, D.A., Dodd, E., Harris, M.D., Ames, J.A., Packham, A.E., Conrad, P.A., 2002. Coastal freshwater runoff is a risk factor for *Toxoplasma gondii* infection of southern sea otters (*Enhydra lutris nereis*). *Int. J. Parasitol.* 32, 997–1006.
- Müller, T., Selhorst, T., Schuster, P., Vos, A., Wenzel, U., Neubert, A., 2002. Kinetics of maternal immunity against rabies in fox cubs (*Vulpes vulpes*). *BMC Infect. Dis.* 2, 10., www.biomedcentral.com.
- Nokes, D.J., 1993. Modelling toxoplasma incidence from longitudinal seroprevalence in Stockholm, Sweden. *Parasitology* 107, 33–40.
- Oksanen, A., Åsbakk, K., Nieminen, M., Norberg, H., Näreaho, A., 1997. Antibodies against *Toxoplasma gondii* in Fennoscandian reindeer—association with the degree of domestication. *Parasitol. Int.* 46, 255–261.
- Oksanen, A., Tryland, M., Johnsen, K., Dubey, J.P., 1998. Serosurvey of *Toxoplasma gondii* in North Atlantic marine mammals by the use of agglutination test employing whole tachyzoites and dithiothreitol. *Comp. Immunol. Microbiol. Infect. Dis.* 21, 107–114.
- Owen, M., Gullestad, N., 1984. Migration routes of Svalbard barnacle geese *Branta leucopsis* with a preliminary report on the importance of the Bjørnøya staging area. *Norsk Polarinstittutt Skrifter* 181, 67–77.
- Prestrud, P., 1992. Food-habits and observations of the hunting behaviour of arctic foxes, *Alopex lagopus*, in Svalbard. *Can. Field-Nat.* 106, 225–236.
- Prestrud, P., Nilssen, K., 1992. Fat deposition and seasonal variation in body composition of arctic foxes in Svalbard. *J. Wildl. Manag.* 56, 221–233.
- SCRIB., 2007. Seabird Colony Registry of the Barents and White Seas. Unpublished database, Norwegian Polar Institute.
- Sørensen, K.K., Mørk, T., Sigurðardóttir, Ó.G., Åsbakk, K., Åkerstedt, J., Bergsjø, B., Fuglei, E., 2005. Acute toxoplasmosis in three wild arctic foxes (*Alopex lagopus*) from Svalbard; one with co-infections of *Salmonella* Enteritidis PT 1 and *Yersinia pseudotuberculosis* serotype 2b. *Res. Vet. Sci.* 78, 161–167.
- Strøm, H., 2006. Birds of Svalbard. In: Kovacs, K.M., Lydersen, C. (Eds.), *Birds and mammals of Svalbard. Polarhåndbok* No. 13. Norwegian Polar Institute, Tromsø, Norway, pp. 85–185.
- Tryland, M., Handeland, K., Bratberg, A.-M., Solbakk, I.-T., Oksanen, A., 2006. Persistence of antibodies in blood and body fluids in decaying fox carcasses, as exemplified by antibodies against *Microsporium canis*. *Acta Vet. Scand.* 48, 10., www.actavets-cand.com.
- Veit, P., Bilger, B., Schad, V., Schäfer, J., Frank, W., Lucius, R., 1995. Influence of environmental factors on the infectivity of *Echinococcus multilocularis* eggs. *Parasitology* 110, 79–86.
- Wanha, K., Edelhofer, R., Gabler-Eduardo, C., Prosl, H., 2005. Prevalence of antibodies against *Neospora caninum* and *Toxoplasma gondii* in dogs and foxes in Austria. *Vet. Parasitol.* 128, 189–193.