Endoparasites of Arctic Wolves in Greenland ULF MAROUARD-PETERSEN¹

(Received 20 February 1997; accepted in revised form 12 August 1997)

ABSTRACT. Fecal flotation was used to evaluate the presence of intestinal parasites in 423 wolf feces from Nansen Land, North Greenland (82°55'N, 41°30'W) and Hold with Hope, East Greenland (73°40'N, 21°00'W), collected from 1991 to 1993. The species diversity of the endoparasitic fauna of wolves at this high latitude was depauperate relative to that at lower latitudes. Eggs and larvae of intestinal parasites were recorded in 60 feces (14%): Nematoda (roundworms) in 11%; Cestoda (flatworms of the family Taeniidae) in 3%. Four genera were recorded: *Toxascaris, Uncinaria, Capillaria*, and *Nematodirus*. Eggs of taeniids were not identifiable to genus, but likely represented *Echinococcus granulosus* and *Taenia hydatigena*. The high prevalence of nematode larvae may be a consequence of free-living species' invading the feces. The occurrence of taeniids likely reflects the reliance of wolves on muskoxen for primary prey. This is the first quantitative study of the endoparasites of wolves in the High Arctic.

Key words: arctic wolves, endoparasites, Greenland, helminths, High Arctic, muskoxen

RÉSUMÉ. On a utilisé la flottation coproscopique afin d'évaluer la présence de parasites intestinaux dans 423 excréments de loups prélevés de 1991 à 1993 à Nansen Land dans le Groenland septentrional (82°55'de latit. N., 41°30' de latit. O.) et à Hold with Hope dans le Groenland oriental (73°40' de latit. N, 21°00' de latit. O.). La diversité des espèces de la faune endoparasite des loups à cette haute latitude était peu importante par rapport à celle de latitudes plus basses. On a noté la présence d'oeufs et de larves de parasites intestinaux dans 60 excréments (14 p. cent): nématodes (vers ronds) dans 11 p. cent; cestodes (vers plats de la famille du ténia) dans 3 p. cent. On a relevé 4 genres: *Toxascaris, Uncinaria, Capillaria* et *Nematodirus*. On n'a pas pu relier les oeufs de ténias à des genres, mais ils représentaient probablement *Echinococcus granulosus* et *Taenia hydatigena*. La fréquence élevée de larves de nématodes peut être une des conséquences d'espèces libres qui envahissent les excréments. La présence de taenidae reflète vraisemblablement la dépendance du loup sur le boeuf musqué en tant que proie principale. Cette étude représente le premier travail quantitatif sur les endoparasites du loup dans l'Extrême-Arctique.

Mots clés: loups arctiques, endoparasites, Groenland, helminthes, Extrême-Arctique, boeuf musqué

Traduit pour la revue Arctic par Nésida Loyer.

INTRODUCTION

Studies of helminth (parasitic worm) fauna of wolves, Canis lupus L., in temperate and subarctic regions have documented that wolves serve as final hosts for a variety of helminths (Rausch and Williamson, 1959; Holmes and Podesta, 1968; Samuel et al., 1978; McNeill et al., 1984). Helminths occurring in wolves include trematodes (9 species recorded), cestodes (21 species) and nematodes (24 species) (Mech, 1970). No comprehensive studies have been conducted on helminths of wolves (Canis lupus arctos Pocock) inhabiting the High Arctic, but incidental observations have been made. Taenia sp. occurred in a wolf killed between Greenland and Ellesmere Island (Nares, 1878). Trichinella spiralis occurred in tissue adhering to two of four wolf pelts from northwestern Greenland (Madsen, 1961). Taenia spp. and Toxascaris leonina were recorded in 97% of 89 wolves from the Yukon and 80% of 61 wolves from the Northwest Territories, including two from Ellesmere Island (Choquette et al., 1973). These appear to be the only studies reporting helminths of wolves in the High Arctic.

Investigations of the helminth fauna of wolves have documented a decrease in species diversity with increasing latitude (Choquette et al., 1973), commonly seen in other biota. These authors reported that species composition in tundra wolves in the Northwest Territories was more homogenous than that of wolves at lower latitudes, likely because of severe environmental conditions and lack of appropriate intermediate hosts in the Arctic. Eggs of many helminths are unable to survive for long in areas of high solar radiation and low yearly precipitation (Dunn, 1978), characteristics of the High Arctic. Furthermore, many helminth species and their intermediate hosts cannot tolerate the cold of the High Arctic. Wolves there occur at the lowest recorded densities (Riewe, 1977), probably resulting in less social stress and decreased contamination of the environment, important factors in reducing prevalence of parasite burdens.

The present study is the first survey of helminths of wolves in the High Arctic. As part of a general study of the ecology of arctic wolves in Greenland, this investigation was undertaken to identify parasites, to describe the

¹ Greenland Wolf Research Project, 3701 Beeman Circle, Anchorage, Alaska 99507, U.S.A. © The Arctic Institute of North America diversity of parasitic species, and to compare the findings with those of studies performed in lower latitudes. I conjectured that: (1) species diversity of the helminth fauna of wolves at this high latitude would prove depauperate relative to that of lower latitudes; (2) only cold-tolerant and desiccation-resistant species of helminths would occur, and (3) evidence of parasites in wolf feces would be limited because of rapid desiccation and a hypothesized low prevalence rate. In Greenland, more than 90% of wolf range falls within the boundaries of the Northeast Greenland National Park (Fig. 1) where the wolf population was estimated at fewer than 75 animals (Marquard-Petersen, 1995). Inside the park, the killing of wolves for scientific study is not allowed by Greenland authorities. Harvest outside the park-in Jameson Land, by Inuit from Ittoqqortoormiit (Fig. 1)—is irregular and insignificant.

MATERIALS AND METHODS

The present investigation employed fecal examination to determine the presence of helminths. This procedure, which involved collecting feces and analyzing them using fecal flotation, has been used successfully where population size was small and wolves were too valuable to be killed (Byman et al., 1977; Archer et al., 1986; Phillips and Scheck, 1991). A total of 423 wolf feces of undetermined age were collected opportunistically on summer and winter range in Nansen Land, North Greenland and Hold with Hope, East Greenland (Fig. 1). Both study areas are located in the High Arctic and are characterized by high alpine terrain with numerous glaciers. Nansen Land is considered true polar semidesert, with an annual precipitation of less than 100 mm and a mean annual temperature of -16°C (Klein and Bay, 1994). Foged (1955) measured regional humidity in nearby Peary Land at 30% and maximum temperature (August) at 16.7°C. Hold with Hope has a higher degree of vegetative cover, with widespread tundra. The nearest weather station has reported a mean annual precipitation of 285 mm and a mean annual temperature of -9°C (Klein and Bay, 1990). Because feces could not be examined immediately, many nematode larvae and some eggs were in poor condition and too dessicated to be suitable for detailed study. In the laboratory, feces from Nansen Land were autoclaved (20 minutes, 123°C) for safety reasons during analysis of this sample for a related study of food habits (Marquard-Petersen, in press). A comparative analysis of 22 feces from wolves suggested that this procedure did not influence detectability of helminth eggs and larvae. Feces from Hold with Hope were not autoclaved. Feces were examined using an Ovatector Kit® (BGS Medical Products, Venice, Florida) and the flotation methods described by Ewing (1986:375), using sodium nitrate (specific gravity 1.30) as a flotation medium. A cover slip measuring 25 mm by 25 mm was positioned on top of the flotation apparatus and examined in its entirety after 15 minutes, using a calibrated micro-

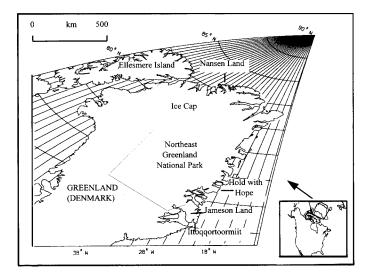


FIG. 1. Greenland, showing areas identified in the text.

scope at 100× magnification. Specimens were recorded on film using a calibrated Olympus BH-2 photomicrographic system, and on video using a standard HI-8 camcorder. Helminths were identified by locating eggs and larvae adhering to slides, obtaining their dimensions, and comparing them with descriptions by Soulsby (1982), Spencer and Monroe (1982), Sloss et al. (1994), and Bowman (1995). Eggs were identified to genus or species. The desiccated condition of the material permitted nematode larvae to be identified only to class. Eggs of Taeniidae (possibly Taenia spp., Echinococcus spp.) cannot be distinguished and were reported under family. Helminths were scored on the basis of their presence or absence within the overall sample, but prevalence rates for the population could not be calculated, because it was unknown how many wolves were represented by the 423 fecal samples.

RESULTS

Nansen Land, North Greenland (n = 72)

Eggs and larvae occurred in 44% (n = 32) of feces from wolves. A minimum of three genera were represented: Nematoda: *Toxascaris leonina* and *Capillaria* sp.; Cestoda: representatives of the family Taeniidae (Table 1).

The class Nematoda was represented in 39% (n = 28) of the feces. This class was dominated by the occurrence of larvae in 23 feces at a mean density of 2.9 larvae per cover slip (range 1–9). Some larvae were tightly coiled, obscuring diagnostic features. Mean length was 277 μ m (range 167–478 μ m, n = 22). Mean width at mid-gut level was 22 μ m (range 14–38 μ m). The species observed as eggs were *Toxascaris leonina* and *Capillaria* sp.

Members of Cestoda occurred in 18% (n = 13) of the feces. This class was represented exclusively by Taeniidae. Mean number of taeniid eggs per slide, excluding a fecal sample

Taxon	Nansen Land ¹ ($N = 72$)	Hold with Hope $(N = 351)$	Total no. of feces infected	Total % of feces infected
Unidentified Nematoda	23	11	34	8.0
Taeniidae	13	8	21	5.0
Toxascaris leonina	4	4	8	1.9
Nematodirus helvetianus	-	1	1	<1
Uncinaria sp.	-	4	4	<1
Capillaria sp.	1	-	1	<1
Total	41	28	69	-

TABLE 1. Helminth eggs and larvae in 423 wolf feces from two areas in Greenland, 1991–93.

¹ Only 32 feces contained eggs and/or larvae, but some contained more than one species.

containing more than 1000 eggs, was 1.8 eggs per slide; range 1-1000+.

Hold with Hope, East Greenland (n = 351)

Only 8% (n = 28) of the feces contained eggs or larvae, with a minimum of four genera represented (Table 1): Nematoda: *Toxascaris leonina, Uncinaria* cf. *stenocephala*, and *Nematodirus* sp.; Cestoda: representatives of Taeniidae.

The class Nematoda was represented in 6% (n = 20) of the feces, dominated by the occurrence of 48 larvae in 11 feces at a density of 4.4 larvae per cover slip (range 1–35). Mean length was 479 μ m (range 357–729 μ m, n = 10). Mean width at mid-gut level was 29 μ m (range 21–42 μ m). No live larvae were observed. Species observed as eggs were *Toxascaris leonina, Uncinaria* sp., and *Nematodirus helvetianus*. Eggs of taeniids occurred in 2% (n = 8) of the feces. Maximum number of taeniid eggs per slide was 59 (mean: 11, range 1–59).

DISCUSSION

The species diversity of helminths of wolves in North and East Greenland was found to be relatively depauperate compared with that of wolves at lower latitudes. Fresh feces contained little parasitic material. Ignoring eggs of Taeniidae, not identifiable to genus, only three species occurring in wolves were recorded: Toxascaris leonina, Uncinaria sp., and Capillaria sp. This finding supports the notion of Choquette et al. (1973) that species diversity of helminths in wolves decreases with increasing latitude. Other than Taeniidae, four helminth species have been found in tundra wolves from the Northwest Territories; five species in wolves from the boreal region of the Yukon (Choquette et al., 1973); and seven species in wolves from Alberta (Holmes and Podesta, 1968). A similar decrease in species diversity of parasites with increasing latitude was reported in arctic fox in Greenland (Kapel and Nansen, 1996).

Nematodes were the most common of all helminths. This finding was unexpected, as studies from lower latitudes have documented that Cestoda (*Taenia* spp., *E. granulosus*) dominated infections in wolves (Erickson, 1944; Rausch and Williamson, 1959; Holmes and Podesta, 1968). Those prevalence rates may not be directly comparable with data from the

present study, because it was unknown how many individual wolves were represented by the feces.

Eggs of *Toxascaris leonina* occurred in feces from both study areas. Rausch et al. (1983) found this nematode to be ubiquitous in arctic canids. *Toxascaris* has been recorded in 84% of 162 wolves from northern Alaska (Rausch and Williamson, 1959), in both of two wolves from Ellesmere Island, and in 80% of 61 wolves from the Northwest Territories (Choquette et al., 1973). In Greenland, this parasite has been found in 39% of 38 (Rausch et al., 1983) and 58% of 254 (Kapel and Nansen, 1996) arctic foxes, respectively. *T. leonina* is less prevalent in lower latitudes; it occurred in 14% of 98 necropsied wolves from Alberta (Holmes and Podesta, 1968), but eggs of this species were not identified in 204 feces from Minnesota (Byman et al., 1977).

Rodents are widely recognized to act as hosts, but little was known about the helminthic fauna of collared lemming, *Dicrostonyx groenlandicus* Traill, in Greenland. In the present study, the low prevalence of *T. leonina* correlated with the low occurrence of lemming remains in 461 wolf feces (10.2– 11.4%; Marquard-Petersen, in press).

Uncinaria sp. occurred in feces from Hold with Hope, but not in those from Nansen Land. Rausch et al. (1983) found the nematode *U. stenocephala* to be common in canids in northern regions. In other studies, this parasite was found in 7% of 200 wolves in Alaska (Rausch and Williamson, 1959), and 11% of 89 wolves from the Yukon, but was not found in 61 tundra wolves from the Northwest Territories (Choquette et al., 1973). It has been found in sled dogs (*Canis familiaris* L.) on Ellesmere Island (Cameron et al., 1940). In Greenland, it had been recorded only once before, represented by a single specimen in one of 38 arctic foxes (Rausch et al., 1983). It was not reported in Kapel and Nansen's (1996) study of 254 foxes.

Eggs and larvae were resistant to freezing (Balasingam, 1964). In Hold with Hope, during July 1992 and 1993, temperatures above 7.5°C were common (away from the coast), suggesting that development to the infective stage could take place in July. Optimal conditions for egg development occurred in sandy, moist loam (Levine, 1980). Some wolf dens in Hold with Hope are dug in sandy loam (Marquard-Petersen, 1994) that is kept moist during summer by underlying permafrost. Conditions therefore appeared suitable for wolves to become infected at an early age at den sites. Because no development to the infective stage occurred

under 7.5°C, many areas in the Arctic are probably not suitable for development of the free-living stage.

Capillaria sp. was represented in feces from Nansen Land. This was apparently the first record of this nematode from Greenland. *C. aerophila* Creplin, 1839, has been found in the mucosa of the respiratory system of wolves, but is not common. Holmes and Podesta (1968) recorded this parasite in 1% of 98 wolves from Alberta. *Capillaria* spp. occurred in 1% of 204 wolf feces from northeastern Minnesota (Byman et al., 1977), and in 6% of 71 feces from Wisconsin (Archer et al., 1986). *C. plica* (Rudolphi, 1819) occurred in wolves from the Mordovan Soviet Socialist Republic (Shaldybin, 1957), and *C. hepatica* (Bancroft, 1893) was noted in brown lemmings (*Lemmus sibiricus* Swarth) in Alaska by Rausch (1961:18), who concluded that this nematode was "a member of the arctic fauna." Its eggs could occur in wolf feces if a rodent were taken as prey.

An egg of *Nematodirus* cf. *helvetianus* occurred in a single wolf feces from Hold with Hope. This nematode is not known to parasitize wolves, but is characteristic of the muskox (*Ovibos moschatus* Zimmermann) in the Canadian Arctic (Samuel and Gray, 1974; Webster and Rowell, 1980) and was reported from all of five muskoxen from West Greenland by Korsholm and Olesen (1993). The feces in which this nematode occurred contained remains of muskox, suggesting that this occurrence was related to a wolf's ingesting the intestinal tract of the ungulate.

The occurrence of nematode larvae in feces was unexpected. Larvae were often missed in standard flotation tests because their large mass relative to eggs caused larvae to sink to the bottom of the flotation apparatus. There were significant differences in larval sizes between areas, as demonstrated by measurements of larvae for which complete data could be obtained. Larvae from Nansen Land (n = 22) were shorter (mean: 277 μ m) and narrower (mean = 22 μ m) than larvae from Hold with Hope (n = 10, mean length = 479 μ m, mean width = $29 \,\mu$ m). Since the larvae could not be identified to genus, this variation is not easily explained. However, the number of nematodes with larval stages occurring in wolf feces was probably limited to the following nematodes: Ancylostoma spp., Uncinaria stenocephala, Crenosoma vulpis (Dujardin, 1844), Filaroides osleri (Cobbold, 1879), Trichinella spp., and free-living nematodes.

Some of these helminths were excluded from further consideration because of ecological factors. Thus, the larvae observed may represent *Uncinaria stenocephala*, *Trichinella* spp., or other unknown species. However, only two larvae matched the measurements of *U. stenocephala* larvae reported by Gibbs (1961), and no larvae matched the measurements of *Trichinella* larvae by Khan (1966). It is therefore concluded that the high occurrence of nematodes may have been a consequence of free-living species' having invaded feces, and thus did not reflect dominance of Nematoda in wolves.

Cestoda was represented by Taeniidae. Eggs occurred in 5% of 423 feces. Cestodes were thus recorded more frequently than eggs of any other helminths. A total of 13 *Taenia*

spp. and two *Echinococcus* spp. were reported in wolves by Mech (1970). In the Arctic, *Taenia* spp. were recorded in 91% of 200 wolves from Alaska by Rausch and Williamson (1959), and in 81% of 171 wolves from the Yukon and the Northwest Territories, including one of two wolves from Ellesmere Island (Choquette et al., 1973). *Echinococcus granulosus* was also reported in 30% of 200 wolves from Alaska (Rausch and Williamson, 1959) and 22% of 89 wolves from the Yukon (Choquette et al., 1973).

Wolves contract infections with both genera through predation on an intermediate host, typically a cervid. *Taenia* spp. has been reported in muskoxen (Fielden, 1877), and *T. hydatigena* occurred in three of three muskoxen from the Thelon Game Sanctuary, Northwest Territories studied by Gibbs and Tener (1958). Taeniids also occurred in two of five muskoxen from Ellesmere Island (Webster and Rowell, 1980), and *E. granulosus* occurred in the lungs of a muskox from Ellesmere Island (Tener, 1965) and in one from the Thelon Game Sanctuary (Gibbs and Tener, 1958). Taeniids may also develop in lagomorphs and rodents.

The principal intermediate host of taeniids has been found to be the herbivorous mammal constituting the primary prey of the final host (Rausch, 1994). This suggests that taeniid infection is primarily contracted through predation on muskoxen, because this ungulate overwhelmingly constitutes the main prey of wolves in Greenland (Marguard-Petersen, in press). In the predator-prey system, each mammalian species may act respectively as final and intermediate host for as many as three different taeniid species; in the wolf, these are typically T. hydatigena, T. ovis krabbei, and E. granulosus (Rausch, 1994). Eggs identified as Taeniidae may therefore represent two different genera and several species, but given the occurrence of T. hydatigena and E. granulosus in muskoxen, it is almost certain that these species were present. Previous studies suggested that E. multilocularis rarely occurred in wolves. Because eggs representing Taeniidae could not be differentiated, no further identification was possible.

Only 14% of 423 feces contained parasitic material, suggesting that evidence of parasites in wolf feces from Greenland was limited. Nonetheless, additional work would be necessary to identify the principal causes: low prevalence in the wolf population, the effects of a severe environment, the fact that many helminths may not be at the egg-laying stage, or a combination of these and other factors.

Extreme cold is lethal to helminth eggs and larvae, but in the microclimate underneath the snow, where temperature may be close to 0°C, eggs and larvae may survive the arctic winter. However, some localities I visited during 1900 km of ground surveys in North Greenland during May 1995 were devoid of snow, indicating that helminth eggs and larvae on the ground in certain areas may not have had snow cover for insulation against the extremely low temperatures common in winter, or for protection against ultraviolet radiation. Although helminth species documented here were considered cold-tolerant, this exposure to extreme cold and solar radiation was likely to act as a limiting factor. Furthermore, low humidity and lack of precipitation in North Greenland probably caused rapid desiccation of helminth eggs and larvae. This desiccation was highly lethal to most helminth species. Environmental conditions in North Greenland may not be favorable for continuing the helminth cycle between wolves and their prey, except in those helminth species not requiring a free-living stage. This hypothesis may offer a partial explanation of why overall evidence of helminths was low and taeniids were observed more frequently than other helminths. Species capable of infecting their host through autoinfection were also likely to prevail in this environment. In Hold with Hope, the increased yearly precipitation relative to North Greenland, and the relatively moderate temperatures, may have offered a more favorable environment for helminth larvae and eggs. This notion might explain why Uncinaria spp. was observed in feces from Hold with Hope but not in feces from Nansen Land.

No helminths were observed in 86% of the feces, but this did not necessarily imply that these wolves were not infected. The flotation procedure was most effective if fecal samples were fresh. The study included older feces, and since organic matter breaks down slowly in the High Arctic, some may have been several years old. This may have adversely affected the analysis, as most helminths and their eggs were likely unable to survive for long in the desert-like conditions characteristic of parts of Greenland. Dehydration of older feces may therefore have biased the flotation procedure, causing me to underestimate the helminth prevalence in feces. Helminth eggs also may be produced only periodically, therefore escaping detection in fecal flotation. Nevertheless, eggs of some helminths had extreme resiliency and were detectable even in older feces. For example, eggs of E. granulosus can withstand freezing and drying on the ground for approximately a year (Sweatman and Williams, 1963). Given the coevolutionary history of helminths, wolves, and their prey in the High Arctic, helminth species in North Greenland may have developed unusual resistance to factors in the microclimate which ordinarily are lethal, for example drying and cold.

Helminths reported during this study indicated that the diet of wolves in Greenland is dominated by muskox. The findings, which support those of Choquette et al. (1973), suggest that in the Arctic, representatives of Taeniidae and T. leonina are among the predominant helminths of wolves, likely because of a severe arctic environment. Data presented here represent a conservative estimate of parasites of wolves in Greenland. Some species may have escaped detection because of procedural constraints. The fecal flotation method could be improved by exclusive use of fresh feces collected at active wolf dens with habituated wolves, and by administration of a taeniacide to promote expulsion of adult helminths. This procedure would make possible species identification of Taeniidae and provide additional evidence of intestinal parasites. Future studies on the helminths of arctic hare, lemming, and muskox in North and East Greenland may help answer questions raised here. Permits have previously been issued, allowing

killing of arctic hare and lemming for scientific study, and helminthological studies of muskox could be completed outside the National Park on animals harvested in Jameson Land by Inuit from Ittoqqortoormiit.

ACKNOWLEDGEMENTS

The author acknowledges the invaluable help of R.L. Rausch in the identification of helminth eggs, and the generous assistance provided by E.H. Follmann. I appreciate the efforts of J.E. Blake, R.T. Bowyer, E.H. Follmann, R.L. Rausch, and three anonymous reviewers who offered comments and suggestions on earlier drafts of the manuscript.

REFERENCES

- ARCHER, J., TAFT, S.J., and THIEL, R.P. 1986. Parasites of wolves, *Canis lupus*, in Wisconsin, as determined from fecal examinations. Proceedings of the Helminthological Society of Washington 53:290–291.
- BALASINGAM, E. 1964. Comparative studies of the effects of temperature on free-living stages of *Placoconus lotoris*, *Dochmoides stenocephala* and *Ancylostoma caninum*. Canadian Journal of Zoology 42:907–918.
- BOWMAN, D.D. 1995. Georgi's parasitology for veterinarians. Philadelphia: W.B. Saunders.
- BYMAN, D., BALLENBERGHE, V.v., SCHLOTTHAUER, J.C., and ERICKSON, A.W. 1977. Parasites of wolves, *Canis lupus* L., in northeastern Minnesota, as indicated by analysis of fecal samples. Canadian Journal of Zoology 55:376–380.
- CAMERON, T.W.M., PARNELL, I.W., and LYSTER, L.L. 1940. The helminth parasites of sledge-dogs in northern Canada and Newfoundland. Canadian Journal of Research 18:325–332.
- CHOQUETTE, L.P.E., GIBSON, G.G., KUYT, E., and PEARSON, A.M. 1973. Helminths of wolves, *Canis lupus* L., in the Yukon and N.W.T. Canadian Journal of Zoology 51:1087–1091.
- DUNN, A.M. 1978. Veterinary helminthology. London: William Heinemann Medical Books Ltd.
- ERICKSON, A.B. 1944. Helminths of the Minnesota Canidae in relation to food habits, and a host list and key to the species reported from North America. American Midland Naturalist 32:358–372.
- EWING, S.A. 1986. Examinations for parasites. In: Coles, E.H., ed. Veterinary clinical pathology. Philadelphia: W.B. Saunders Company.
- FIELDEN, H.W. 1877. Notes on the natural history. In: Nares, G.S., ed. Narrative of a voyage to the Polar Sea during 1875–76 in H.M.S. 'Alert' and 'Discovery.' London: Samson, Low, Marston, Searle and Rivington. Vol. 2. 198–202.
- FOGED, N. 1955. Diatoms from Peary Land, North Greenland. Meddelelser om Grønland 128. 117 p.
- GIBBS, H.C. 1961. Studies on the life cycle and developmental morphology of *Dochmoides stenocephala* (Railliet, 1884) (Ancylostomidae: Nematoda). Canadian Journal of Zoology 39: 325–348.

- GIBBS, H.C., and TENER, J.S. 1958. On some helminth parasites collected from the musk ox (*Ovibos moschatus*) in the Thelon Game Sanctuary, N.W.T. Canadian Journal of Zoology 36: 529–532.
- HOLMES, J.C., and PODESTA, R. 1968. The helminths of wolves and coyotes from the forested regions of Alberta. Canadian Journal of Zoology 46:1193–1204.
- KAPEL, C.M.O., and NANSEN, P. 1996. Gastrointestinal helminths of arctic foxes (*Alopex lagopus*) from different bioclimatological regions in Greenland. Journal of Parasitology 82:17–24.
- KHAN, Z.A. 1966. The postembryonic development of *Trichinella* spiralis with special reference to ecdysis. Journal of Parasitology 52:248–259.
- KLEIN, D.R., and BAY, C. 1990. Foraging dynamics of muskoxen in Peary Land, northern Greenland. Holarctic Ecology 13: 269–280.
- ———. 1994. Resource partitioning by mammalian herbivores in the High Arctic. Oecologia 97:439–450.
- KORSHOLM, H., and OLESEN, C.R. 1993. Preliminary investigations of the parasite burden and distribution of endoparasite species of muskox (*Ovibos moschatus*) and caribou (*Rangifer tarandus groenlandicus*) in West Greenland. Rangifer 13:185–189.
- LEVINE, N.D. 1980. Nematode parasites of domestic animals and man. Minneapolis: Burgess Publishing Co.
- MADSEN, H. 1961. The distribution of *Trichinella spiralis* in sledge dogs and wild mammals in Greenland under a global aspect. Meddelelser om Grønland 159(7). 124 p.
- MARQUARD-PETERSEN, U. 1994. Dens and summer pack size of arctic wolves in Hold with Hope, East Greenland. Polar Record 30:46–49.
- ——. 1995. Status of wolves in Greenland. In: Carbyn, L.N., Fritts, S.H., and Seip, D., eds. Ecology and conservation of wolves in a changing world. Edmonton: Canadian Circumpolar Institute. 55–58.
- ------. In press. Food habits of arctic wolves in Greenland. Journal of Mammalogy.
- McNEILL, M.A., RAU, M.E., and MESSIER, F. 1984. Helminths of wolves (*Canis lupus* L.) from southwestern Quebec. Canadian Journal of Zoology 62:1659–1660.
- MECH, L.D. 1970. The wolf: The ecology and behavior of an endangered species. New York: The Natural History Press.

- NARES, G.S. 1878. Narrative of a voyage to the Polar Sea during 1875–76 in H.M. ships 'Alert' and 'Discovery.' London: Sampson, Low, Marston, Searle, and Revington.
- PHILLIPS, M.K., and SCHECK, J. 1991. Parasitism in captive and reintroduced red wolves. Journal of Wildlife Diseases 27: 498–501.
- RAUSCH, R.L. 1961. Notes on the occurrence of *Capillaria hepatica* (Bancroft, 1893). Proceedings of the Helminthological Society of Washington 28:17–18.
- ———. 1994. Transberingian dispersal of cestodes in mammals. International Journal for Parasitology 28:1203–1212.
- RAUSCH, R.L., and WILLIAMSON, F.S.L. 1959. Studies on the helminth fauna of Alaska. 34. The parasites of wolves, *Canis lupus* L. Journal of Parasitology 45:395–403.
- RAUSCH, R.L., FAY, F.H., and WILLIAMSON, F.S.L. 1983. Helminths of the arctic fox, *Alopex lagopus* (L.), in Greenland. Canadian Journal of Zoology 61:1847–1851.
- RIEWE, R.R. 1977. The high arctic wolf in the Jones Sound region of the Canadian High Arctic. Arctic 28:209–212.
- SAMUEL, W.M., and GREY, D.R. 1974. Parasitic infection in muskoxen. Journal of Wildlife Management 38:775-782.
- SAMUEL, W.M., RAMALINGAM, S., and CARBYN, L.N. 1978.
 Helminths in coyotes (*Canis latrans* Say), wolves (*Canis lupus* L.), and red foxes (*Vulpes vulpes* L.) of southwestern Manitoba.
 Canadian Journal of Zoology 56:2614–2617.
- SHALDYBIN, L.S. 1957. Parasitic worms of wolves in the Mordvinian ASSR. Uch. Zap. Gor'kovsk. Gos. Ped. Inst. 19: 65–70. (From Biological Abstracts 35:2241, No. 25505.)
- SLOSS, M.W., KEMP, R.L., and ZAJAC, A.M. 1994. Veterinary clinical parasitology. Ames: Iowa State University Press.
- SOULSBY, E.J.L. 1982. Helminths, arthropods and protozoa of domesticated animals. Philadelphia: Lea and Febiger.
- SPENCER, F.M., and MONROE, L.S. 1982. The color atlas of intestinal parasites. Springfield: C.C. Thomas Publisher.
- SWEATMAN, G.K., and WILLIAMS, R.J. 1963. Survival of *Echinococcus granulosus* and *Taenia hydatigena* eggs in two extreme climatic regions of New Zealand. Research in Veterinary Science 4:199–216.
- TENER, J.S. 1965. Muskoxen in Canada: A biological and taxonomic review. Ottawa: Queen's Printer.
- WEBSTER, W.A., and ROWELL, J. 1980. Some helminth parasites from the small intestines of free-ranging muskoxen *Ovibos moschatus* (Zimmermann) of Devon and Ellesmere Islands, N.W.T. Canadian Journal of Zoology 58:304–305.