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Source: Journal of Wildlife Diseases, 40(2) : 197-204

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-40.2.197

Journal of Wildlife Diseases, 40(2), 2004, pp. 197–204

MUSKOX LUNGWORM (*UMINGMAKSTRONGYLUS PALLIKUUKENSIS*) DOES NOT ESTABLISH IN EXPERIMENTALLY EXPOSED THINHORN SHEEP (*OVIS DALLI*)

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ABSTRACT: Muskoxen (*Ovibos moschatus moschatus*) on the northwestern mainland of Nunavut and Northwest Territories, Canada, are infected with the protostrongylid lungworm, *Umingmakstrongylus pallikuukensis.* The geographic range of this muskox population is expanding to the south and west, and it is anticipated that these animals will eventually become sympatric with Dall's sheep (*Ovis dalli dalli*) in the Mackenzie and Richardson Mountains. To address the concern of wildlife managers that *U. pallikuukensis* may infect and adversely affect Dall's sheep, four Dall's/Stone's (*Ovis dalli stonei*) hybrid lambs and one adult muskox (*Ovibos moschatus wardi*) were each given 100 third-stage larvae of *U. pallikuukensis.* All animals were intensively monitored for 9 mo postinfection (PI) using clinical examinations, fecal analyses, hematology, blood chemistry, and medical imaging. No first-stage larvae of *U. pallikuukensis* were recovered from the lambs, and monitoring revealed no evidence that the parasite had established in any of these animals. First-stage larvae were found in the feces of the muskox beginning at 94 days PI, and typical parasite cysts were visible in lung radiographs at 188 days PI. This study addresses an important management and wildlife health issue associated with the potential for host-switching of pathogens and indicates that it is improbable that thinhorn sheep are suitable hosts for *U. pallikuukensis.*

Key words: Arctic, host-switching, nematode, *Ovibos moschatus, Ovis dalli,* parasite, subarctic.

INTRODUCTION

A major driver of emerging disease is the movement of domestic and wild species to new geographic locations (Daszak et al., 2000). Translocation of animals, natural range expansions, and changes in behavior and distribution associated with climate or habitat perturbations can result in the formation of new inter- and intraspecies associations, thereby increasing the potential for host-switching by pathogens (e.g., see Hoberg et al., 2002). Consequences of host-switching can range from relatively benign (e.g., *Protostrongylus stilesi* in muskoxen [*Ovibos moschatus moschatus*]; Hoberg et al., 2002) to extremely pathogenic (e.g., *Parelaphostrongylus tenuis* in caribou [*Rangifer tarandus*] and moose [*Alces alces*]; see Lankester, 2001). Perhaps more often the effects are subtle but may have profound ecological consequences, such as parasite-mediated competition (Tompkins et al., 2002). Identification of current host and geographic distributions of pathogens and innovative studies to determine the effects in wildlife are crucial for understanding and predicting the potential for pathogen exchange among species and the subsequent impacts on host individuals and populations. In the Canadian north, natural range expansion of muskoxen infected with a potentially pathogenic pulmonary nematode, *Umingmakstrongylus pallikuukensis,* has raised concerns among wildlife managers and stakeholders that this nematode may infect Dall's sheep (*Ovis dalli dalli*) and have possible detrimental effects.

Umingmakstrongylus pallikuukensis is a protostrongylid lungworm that was discovered in 1988 in muskoxen on the western mainland of what is now Nunavut (NU), Canada (Gunn and Wobeser, 1993; Hoberg et al., 1995). Adult parasites are up to

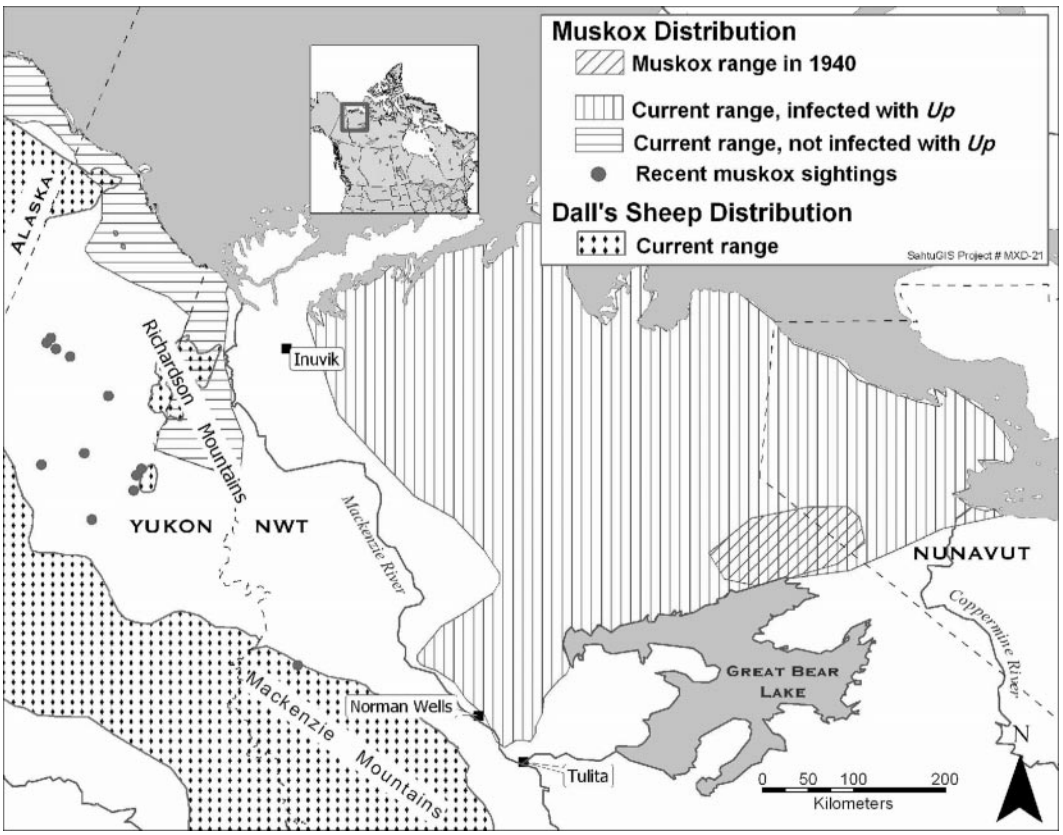

FIGURE 1. Map of muskox and Dall's sheep distribution in eastern Alaska, Yukon, and mainland Northwest Territories and western Nunavut. (Map produced by Miki Promislow and James Auld, Sahtu GIS Project.)

65 cm in length and live in groups of two to seven in cysts, 5–40 mm in diameter in the lungs (Kutz et al., 1999b). The parasites are long-lived (at least 2 yr), and the major lesions are associated with the cysts, which when present in large numbers may occupy considerable lung volume (Kutz et al., 1999b). Anecdotal reports from hunters that animals from the infected population show exercise intolerance and epistaxis suggest that *U. pallikuukensis* may impact the health of individual animals (Hoberg et al., 1995). Population-level effects have not been investigated.

Umingmakstrongylus pallikuukensis is restricted geographically, perhaps in part because of climatic conditions and the historic distribution of muskoxen, to the region of the mainland extending from the Mackenzie River, Northwest Territories (NT), in the west to just east of the Coppermine River, NU, (Fig. 1; Hoberg et al., 1995; Kutz et al., 2004). Muskoxen were almost extirpated from the mainland NT in the early 1900s (Barr, 1991), and these infected animals are thought to be descendants of a remnant population from north of Great Bear Lake (Fournier and Gunn, 1998; Fig. 1). The infected muskoxen continue to colonize regions to the west, and by 2003 approximately 300–350 were considered resident south of the tree line in the area between Great Bear Lake and the Mackenzie River (A. Veitch and R. Popko, unpubl. data). Prevalence of *U. pallikuukensis* in muskoxen in this area is 100% (n=46 fecal samples; A. Veitch and R. Popko, unpubl. data). It is anticipated that these infected muskoxen will eventually cross the Mackenzie River and become

sympatric with Dall's sheep in the Mackenzie and Richardson Mountains immediately to the west (Fig. 1).

Umingmakstrongylus pallikuukensis also appears to have a restricted host range. It has not been found in sympatric cervids such as moose (based on hunter reports) or caribou (based on hunter reports and detailed examination of lungs and/or feces of over 100 animals; Gunn et al., 1991; B. Elkin, S. Kutz, and J. Nishi, unpubl. data). From a phylogenetic perspective, a more probable alternative host for *U. pallikuukensis* in northern Canada may be Dall's sheep. Dall's sheep are more closely related to muskoxen than are the cervids (Hassanin et al., 1998), and *U. pallikuukensis* is closely related to *Cystocaulus* and *Muellerius,* protostrongylid lungworms that are characteristic in *Ovis* spp. (Carreno and Hoberg, 1999).

Common range use by muskoxen and Dall's sheep can result in pathogen exchange between these species. For example, in the northern Yukon and far northwest NT, where Dall's sheep share range with an introduced subspecies of muskox (*Ovibos muschatus wardi*), a protostrongylid lungworm of Dall's sheep, *Protostrongylus stilesi,* has established in the muskoxen. These muskoxen are descendants of a group that was brought to Nunavik Island, Alaska, USA, from Greenland, and are not infected with *U. pallikuukensis* (Hoberg et al., 2002). Presence of *P. stilesi* in these animals indicates 1) muskoxen are susceptible; and 2) climatic conditions, intermediate host availability, and patterns of habitat use between muskoxen and Dall's sheep are adequate for transmission of this protostrongylid from sheep. It follows that other protostrongylid parasites with similar life history patterns may be exchanged between these two host species (discussed in Hoberg et al., 2002). *Umingmakstrongylus pallikuukensis* has a typical protostrongylid life cycle requiring gastropod intermediate hosts for transmission (Kutz et al., 2001a). Preliminary studies in the Mackenzie Mountains indicate that there are suitable gastropod intermediate host species (*Deroceras laeve* and *Catinella* sp.) and climatic conditions for the development of this parasite (E. Jenkins, pers. com.). Thus, it is probable that if range overlap does occur between Dall's sheep and infected muskoxen, the sheep will be exposed to *U. pallikuukensis.*

Addition of *U. pallikuukensis* to the existing pulmonary pathogen fauna of Dall's sheep may have detrimental effects. In the Mackenzie Mountains, Dall's sheep are already infected with two protostrongylid nematodes that cause substantial pulmonary damage (*P. stilesi* and *Parelaphostrongylus odocoilei*) and sheep in the Richardson Mountains are infected with *P. stilesi* (Kutz et al., 2001c). These nematodes cause distinct patterns of pulmonary damage that can range from mild to severe (see Kutz et al., 2001c). The addition of *U. pallikuukensis,* causing a second (Richardson Mountains) or third (Mackenzie Mountains) type of unique damage would be a further pulmonary stressor that could have significant impacts on the Dall's sheep populations. The objective of the current study was to determine if *U. pallikuukensis* can establish in thinhorn sheep (*O. dalli*).

MATERIALS AND METHODS

Lambs used in this study were born between 10 and 27 May 2002 on a Saskatchewan (Canada) game ranch. They were transported to the Western College of Veterinary Medicine, Saskatoon, Saskatchewan, when 16–36 hr old and subsequently bottle-reared so as to minimize the anticipated stress associated with the routine handling necessary during this study. Captive sources of thinhorn lambs are limited, and we were able to obtain only four Dall's/Stone's (*Ovis dalli stonei*) hybrid ewe lambs. Although Dall's and Stone's sheep are considered subspecies (Valdez and Krausman, 1999), there is no mitochondrial genetic evidence to support this designation (D. Coltman, pers. comm.; Ramey, 1993).

Lambs were housed indoors on wood chip bedding until 12 July, on straw until 12 August, and then on wood chips until the study ended. Wet Nurse Ungulate Milk Replacer® (30-30-36; Prairie Micro-Tech Inc., Regina, Saskatchewan, Canada), mixed at one part solid:three parts water, was bottle-fed as per manufactur-

er's recommendations until lambs were weaned on 3 September. Calf Manna® pellets (Manna-Pro, Denver, Colorado; up to 100 $g \cdot day^{-1} \cdot each^{-1}$) were offered until 14 August, and then 12% Zoo Ruminant Pellets (Landmark Feeds Inc., Winnipeg, Manitoba, Canada; 150–200 $g \cdot day^{-1} \cdot each^{-1}$) from 22 August until the end of the study. Lambs were given free choice mixed grass hay until the third week of July when, because of a severe province-wide shortage of grass hay, alfalfa hay was offered. On 12 August a new source of mixed grass hay was found and lambs were maintained on this until the end of the study. Small amounts of fresh browse were provided almost daily from May to September. An adult male castrate muskox (*O. muschatus wardi*) from the University of Saskatchewan research herd was used as a positive control and was housed indoors on rubber mats and fed mixed grass and alfalfa hay and 250 g/day of muskox pellets. All animals were housed and handled according to University of Saskatchewan University Committee on Animal Care and Supply protocol 2002-0025.

The source of the *U. pallikuukensis* used in the study was feces collected in March 2002 from a naturally infected wild muskox in the Sahtu region, NT. Slugs (*D. laeve)* from a captive colony were infected with first-stage larvae (L1) isolated from these feces (Hoberg et al., 1995). Slugs were housed at 20–23 C for 14 days and then digested, and L3 were recovered (Hoberg et al., 1995). One hundred infective L3 (Kutz et al., 2001b) were then randomly assigned to each of five test tubes containing approximately 2 ml of tap water and refrigerated at 4 C overnight. All four lambs, aged 7–9 wk, were given L3 the next day (16 July). Lambs were sedated with an intramuscular injection of 0.1 mg/kg butorphanol (10 mg/ml; Wyeth Animal Health, Guelph, Ontario, Canada) combined with 0.2 mg/kg midazolam (5 mg/ml; Sabex, Boucherville, Quebec, Canada). Once adequate sedation was achieved (approximately 10–15 min postinjection), 100 L3 of *U. pallikuukensis* in 10 ml of tap water were administered to each lamb by stomach tube. The tube was then flushed with 60 ml of air, 60 ml of water, and a final 60 ml of air. The fifth test tube was held in the refrigerator for 10 days, and the L3, in 10 ml of water, were then administered by stomach tube to the muskox (sedated with 0.05 mg/kg of xylazine hydrochloride [Rompun 20 mg/ml Injectable®, Bayer Inc., Toronto, Ontario]), followed by 120 ml of air, 120 ml of water, and 120 ml of air.

Thoracic radiographs (lateral and dorsal-ventral for the lambs, lateral only for the muskox), complete blood counts, serum chemistry, and fresh fecal samples (Baermann examination for protostrongylid L1; Forrester and Lankester, 1997) from all animals were examined during the week prior to infection. Following infection, lambs were monitored daily for changes in respiratory rate and effort. Repeat blood samples were taken from the lambs at 1, 2, and 6 mo postinfection (PI), and follow-up radiographs were taken at approximately 2 mo PI for the lambs (sedation with xylazine hydrochloride 0.1 mg/kg), and 6 and 7 mo PI for the muskox (no sedation). At 6–7 mo PI the lambs' lungs were examined by computed tomography (CT; 1 mm sections; see Kutz et al., 1999a). For this procedure the animals were maintained under general anesthesia. They were premedicated with an intramuscular injection of 1.0 mg/kg Telazole® (100 mg/ml; Fort Dodge Animal Health, Fort Dodge, Iowa, USA) combined with 0.5 mg/kg xylazine hydrochloride induced with intravenous 4 mg/kg propofol (Abbot Laboratories Ltd., St. Laurent, Quebec, Canada) combined with 2 mg/kg ketamine hydrochloride (Vetalar®, Bioniche Animal Health Canada Inc., Belleville, Ontario), administered to effect and then maintained on isoflurane (Abbot Laboratories Ltd.). Repeat CT scans were done at 16–17 mo PI.

Beginning on day 36 PI, pooled lamb feces were examined weekly for L1, then from day 79 PI (lambs) and day 69 PI (muskox) feces were examined three times per week. On fecal sampling days lambs were housed on rubber mats from 8 AM to 12 PM, and then all feces were collected and pooled. Eight 5 g subsamples were examined by beaker Baermann technique for protostrongylid L1 using a single layer of QuickWipes tissue (Scott Paper Ltd., Streetsville, Ontario, Canada; Forrester and Lankester, 1997). Intensive sampling continued until 269 days PI, at which time the lambs were moved outdoors and were periodically individually sampled until 17 mo PI. For the muskox, the feces produced over a 24-hr period were pooled and then 5 g subsamples were examined for L1 (six subsamples were examined until 111 days PI, then three subsamples until the end of the experiment). At 167 days PI the sampling frequency for the muskox was reduced to twice weekly. First-stage larvae obtained from the muskox were confirmed as *U. pallikuukensis* by polymerase chain reaction (PCR) and sequencing of the ITS2 region of ribosomal DNA (G. Appleyard, unpubl. data).

RESULTS

The lambs demonstrated no changes in respiratory rate or effort and no L1 of *U. pallikuukensis* were detected in their feces throughout the monitoring period. The to-

tal and differential white blood cell counts fluctuated during the study period. One lamb (lamb 1) had a mild eosinophilia on the day of infection (2.0×10^9/l, normal for domestic sheep is 0–1.2×10^9/l; Prairie Diagnostic Service [PDS] reference values, Western College of Veterinary Medicine), and at 1 mo (1.6×10^9/l) and 6 mo (1.3×10^9/l) PI; another lamb (lamb 6) had an eosinophilia at 1 wk (2.2×10^9/l) and 1 mo PI (1.4×10^9/l). Eosinophil counts for the other two animals remained within normal limits. Serum chemistry changes were mild and nonspecific for all lambs throughout the study with the exception of elevated sorbitol dehydrogenase (SDH) at 5 wk PI in lambs 1 (37 U/l) and 3 (153 U/l; normal values for domestic sheep, 5–29 U/l, PDS). There was no evidence of lungworm-associated pulmonary disease on the radiographs or the CT scans (see Kutz et al., 1999a).

At 3 wk PI, all four lambs developed rhinitis, facial edema, multifocal small cutaneous facial abscesses, and generalized pruritus. The two lambs with the most severe clinical signs (lambs 2 and 6) were treated with antihistamines (diphenhydramine, Sabex, three treatments 12 hr apart), a single dose of dexamethasone (Sabex), and antibiotics (ceftiofur hydrochloride, Pharmacia Animal Health, Orangeville, Ontario) for 3 days, but there was no apparent response to the treatment. No *Trombicula* sp. mites were seen on physical examination. One week after the start of clinical signs, the bedding was changed from straw to wood chips and the feed from alfalfa to grass hay. Clinical signs resolved within 3 wk.

The muskox began shedding L1 of *U. pallikuukensis* in its feces at 94 days PI and shed L1 continuously until the end of the study. Counts peaked at approximately 133 larvae/g of feces at 245 days PI. One typical *U. pallikuukensis* cyst (Kutz et al., 1999a) was identified on the thoracic radiographs at 188 days PI and a second one at 252 days PI (Fig. 2).

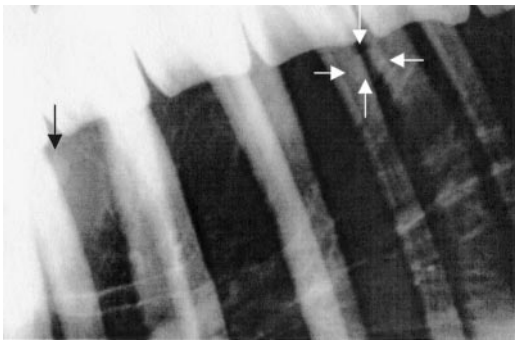

FIGURE 2. Radiograph of muskox lungs with two parasite cysts of *Umingmakstrongylus pallikuukensis* (arrows) at day 252 postinfection (PI).

DISCUSSION

The aim of the present study was to address potential pathogen transmission from an expanding population of muskoxen to Dall's sheep. Results indicate that the protostrongylid lungworm of muskoxen, *U. pallikuukensis*, does not develop to reproductively active adults in experimentally exposed thinhorn lambs. Lambs were monitored intensively for 9 mo, three times the typical prepatent period of this parasite, because protostrongylids in abnormal hosts often have longer prepatent periods than observed in normal hosts (Lankester, 2001).

Viability of larvae used to infect the sheep was confirmed by patent infection of *U. pallikuukensis* in the muskox at 94 days PI (Kutz et al., 1999b). The pattern of larval production was similar to that reported in a previous experimental infection of a muskox receiving 97 L3 (Kutz et al., 1999b), but fecal larval counts in the present study were higher. This may be because the beaker Baermann technique used in the present study (Forrester and Lankester, 1997) is more sensitive than the funnel technique used previously (Kutz et al., 1999b).

Computed tomography, a useful technology for detecting and describing spatial distribution of parasite-induced pulmonary lesions in wildlife (Kutz et al., 1999a), was used in the present study. To detect subtle pulmonary changes, the CT scans were

taken at very high resolution (1-mm sections), and it is likely that even very early cysts of *U. pallikuukensis* (i.e., <5 mm diameter) would have been seen. Absence of detectable abnormalities in the scans at 6–7 mo PI and again at 16–17 mo PI, together with the clinical and fecal examination data, were sufficient to conclude, without postmortem examinations, that *U. pallikuukensis* did not develop to reproductively mature adults in these thinhorn lambs.

The significance of hematology and blood chemistry abnormalities is ambiguous. Increased eosinophil counts at 1 wk and 1 mo PI in only one lamb may have been in response to the parasite challenge, and increases of SDH in two lambs at 5 wk PI, indicative of hepatocellular damage, may also have been associated with parasite migration. Additionally, the episode of rhinitis, pruritus, and facial edema at 3 wk PI, and its possible association with the exposure to *U. pallikuukensis,* remains enigmatic. This episode occurred a few weeks after changes in husbandry from wood chips to straw bedding and a change in feed to alfalfa hay. The room was noticeably dusty during this time period, and fine alfalfa hay particles were seen adherent to the nasal mucosa of the lambs. Resolution of the clinical signs within 3 wk of changing the bedding and hay are suggestive of an environmentally induced atopy or perhaps infection with free-living mites associated with the straw bedding. Because of the limited number of lambs available for this study, there were no negative control animals, and a reaction to larvae of *U. pallikuukensis* cannot be ruled out as a cause of these unusual clinical signs. If the hematologic, serum chemistry, or clinical abnormalities were associated with exposure to L3 of *U. pallikuukensis,* this may have implications for health and survival of thinhorn sheep exposed to this parasite in the wild.

Results from the present study, together with phylogenetic and coevolutionary analyses of the protostrongylids (Carreno and Hoberg, 1999), ongoing surveillance of sympatric species, and attempted experimental infection of domestic sheep (Kutz et al., 1999b) suggest that *U. pallikuukensis* is a host-specific nematode of muskoxen. There are, however, numerous other potential pathogens that may be shared between muskoxen and thinhorn sheep, with unknown ecologic outcomes. Additionally, in captivity or outside of their native range, muskoxen appear to be highly susceptible to the parasites of other ungulate species (Alendal and Helle, 1983). It is, therefore, possible that pathogen exchange between these two hosts may have a more significant impact on muskoxen than Dall's sheep.

It is also plausible that contact and sympatry between muskoxen and Dall's sheep will not negatively affect either species. Currently an *U. pallikuukensis*–free population of introduced muskoxen and native Dall's sheep coexist in northeast Alaska, Yukon Territory, and the Richardson Mountains of the NT, with no apparent negative influence on each other. However, adequate baseline health and population data are not available to properly assess possible pathogen-mediated interactions between these two species. Currently in the Mackenzie Mountains, with the exception of a single sighting of a bull muskox in the northern region (Fig. 1), Dall's sheep and muskoxen remain separate (Veitch et al., 2000). This situation offers a unique opportunity to evaluate transmission of parasites and other pathogens in a changing environment (see Hoberg et al., 2002). Experimental laboratory and field studies, together with surveillance and long-term monitoring aimed at documenting the pathogen fauna and tracking changes and examining epidemiology and effects of pathogens, will provide the scientific foundation to anticipate and assess possible pathogen-mediated competition and other impacts on both host populations.

ACKNOWLEDGMENTS

We thank J. Skific, J. Heaver, E. Jenkins, and the staff of the Animal Care Unit and of Vet-

erinary Anesthesia and Radiology at the WCVM; the staff of the Department of Medical Imaging at the Royal University Hospital, Saskatoon; J. Auld, M. Promislow, B. Elkin, R. Popko, and A. Gunn, Government of the Northwest Territories; and J. Adamczewski and P. Merchant, Government of Yukon. We also thank E. Hoberg and three anonymous reviewers for helpful comments on this manuscript. This project was supported by the Alberta Chapter of the Foundation for North American Wild Sheep; the Association of Mackenzie Mountain Outfitters; the Canadian Cooperative Wildlife Health Centre, Saskatoon; the Department of Resources, Wildlife, and Economic Development, Government of the Northwest Territories, Inuvik and Sahtu Regions; the Gwich'in Renewable Resources Board; the WCVM Muskox Project; and the Wildlife Management Advisory Council (North Slope) and the Government of Yukon.

LITERATURE CITED

ALENDAL, E., AND O. HELLE. 1983. Helminth parasites of muskoxen *Ovibos moschatus* in Norway incl. Spitsbergen and in Sweden, with a synopsis of parasites reported from this host. Fauna Norvegica. Ser A 4:41–52.

BARR, W. 1991. Back from the brink. Komatik series No. 3, The Arctic Institute of North America, Calgary, Alberta, Canada, 127 pp.

CARRENO, R., AND E. P. HOBERG. 1999. Evolutionary relationships among the protostrongylid (Nematoda: Metastrongyloidea) as inferred from morphological characters, with consideration of parasite-host coevolution. Journal of Parasitology 85: 638–648.

DASZAK, P., A. A. CUNNINGHAM, AND A. D. HYATT. 2000. Emerging infectious diseases of wildlife—Threats to biodiversity and human health. Science 287: 443–449.

FORRESTER, S. G., AND M. W. LANKESTER. 1997. Extracting protostrongylid nematode larvae from ungulate feces. Journal of Wildlife Diseases 33: 511–516.

FOURNIER, B., AND A. GUNN. 1998. Muskox numbers and distribution in the Northwest Territories 1997 (file report No. 121). Department of Resources, Wildlife and Economic Development Government of the Northwest Territories Yellowknife, Northwest Territories, Canada, 55 pp.

GUNN, A., AND G. WOBESER. 1993. Protostrongylid lungworm infection in muskoxen, Coppermine, Northwest Territories, Canada. Rangifer 13: 45–47.

———, F. LEIGHTON, AND G. WOBESER. 1991. Wildlife diseases and parasites in the Kitikmeot Region, 1984–1990 (final report No. 104). Department of Renewable Resources, Government of the Northwest Territories, Coppermine, Canada, 52 pp.

HASSANIN, A., E. PASQUET, AND J. D. VIGNE. 1998. Molecular systematics of the subfamily caprinae (Articodactyla, Bovidae) as determined from cytochrome b sequences. Journal of Mammalian Evolution 5: 217–236.

HOBERG, E. P., L. POLLEY, A. GUNN, AND J. S. NISHI. 1995. *Umingmakstrongylus pallikuukensis* gen. nov. et sp. nov. (Nematoda: Protostrongylidae) from muskoxen (*Ovibos moschatus*) in the central Canadian Arctic, with comments on biology and biogeography. Canadian Journal of Zoology 73: 2266–2282.

HOBERG, E. P., S.J. KUTZ, J. NAGY, E. JENKINS, B. ELKIN, M. BRANIGAN, AND D. COOLEY. 2002. *Protostrongylus stilesi* (Nematoda: Protostrongylidae): Ecological isolation and putative host-switching between Dall's sheep and muskoxen in a contact zone. Comparative Parasitology 69: 1–9.

KUTZ, S. J., K. FISHER, AND L. POLLEY. 1999a. A lung nematode in Canadian arctic muskoxen: Standard radiographic and computed tomographic imaging. Veterinary Clinics of North America: Food Animal Practice 15: 359–377.

———, E. P. HOBERG, AND L. POLLEY. 1999b. Experimental infections of muskoxen (*Ovibos moschatus*) and domestic sheep with *Umingmakstrongylus pallikuukensis* (Nematoda: Protostrongylidae): Parasite development, population structure and pathology. Canadian Journal of Zoology 77: 1562–1572.

———, ———, ———. 2001a. A new lungworm in muskoxen: An exploration in Arctic parasitology. Trends in Parasitology 17: 276–280.

———, ———, ———. 2001b. *Umingmakstrongylus pallikuukensis* (Nematoda: Protostrongylidae) in gastropods: Larval morphology, morphometrics, and development rates. The Journal of Parasitology 87: 527–535.

———, A. M. VEITCH, E. P. HOBERG, B. T. ELKIN, E. J. JENKINS, AND L. POLLEY. 2001c. New host and geographic records for two protostrongylids in Dall's sheep. Journal of Wildlife Diseases 37: 761–774.

———, E. P. HOBERG, J. NAGY, AND L. POLLEY. 2004. Emerging parasites in Arctic ungulates. Integrative and Comparative Biology. In press.

LANKESTER, M. W. 2001. Extrapulmonary lungworms of cervids. *In* Parasitic diseases of wild mammals, W. Samuel, M. Pybus, and A. A. Kocan (eds.). Iowa State University Press, Ames, Iowa, pp. 228–278.

RAMEY, R. R. 1993. Evolutionary genetics and systematics of North American mountain sheep: Implications for conservation. PhD Thesis, Cornell University, Ithaca, New York, 251 pp.

TOMPKINS, D. M., D. M. B. PARISH, AND P. J. HUDSON. 2002. Parasite-mediated competition among red-legged partridges and other lowland

gamebirds. Journal of Wildlife Management 66: 445–450.

VALDEZ, R., AND P. R. KRAUSMAN. 1999. Description, distribution, and abundance of mountain sheep in North America. *In* Mountain sheep of North America, R. Valdez and P. R. Krausman (eds.). University of Arizona Press, Tucson, Arizona, pp. 3–22.

VEITCH, A., N. SIMMONS, J. ADAMCZEWSKI, AND R. POPKO. 2000. Status, harvest, and co-management of Dall's sheep in the Mackenzie Mountains, Northwest Territories. Northern Wild Sheep and Goat Council 11: 134–153.

Received for publication 4 June 2003.