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**Authors**

Eric P. Hoberg, Susan J. Kutz, John Nagy, Emily Jenkins, Brett Elkin, Marsha Branigan, and Dorothy Cooley

## ***Protostrongylus stilesi* (Nematoda: Protostrongylidae): Ecological Isolation and Putative Host-Switching Between Dall's Sheep and Muskoxen in a Contact Zone**

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**ABSTRACT:** The occurrence of *Protostrongylus stilesi* in a population of introduced muskoxen, *Ovibos moschatus wardi*, on the Arctic Coastal Plain, Yukon Territory (YT) and Northwest Territories (NT), Canada, is consistent with a contemporary colonization event from Dall's sheep, *Ovis dalli dalli*, which indicates that host specificity may be ecologically based and contextual for this parasite. Colonization of muskoxen by *P. stilesi* may be a predictable event in zones of sympatry with Dall's sheep; exposure to infection may coincide with occupation of winter ranges of Dall's sheep by muskoxen during the summer season. Disruption of contemporary ecological isolating barriers can result from anthropogenically or climatologically driven habitat perturbation, and result from management practices that influence the distribution of ungulate hosts. Thus, if zones of contact become more extensive or the temporal limits on allopatry are relaxed, we may observe increasing instances of host switching by parasites or pathogens at the interface of newly emerging ecotones. Impacts to northern systems linked to climatologically and anthropogenically driven global change and the effects of management must be tracked within the context of biodiversity survey and inventory and archival collections, as foundations for monitoring ecosystem-level perturbations. A developing interface for muskoxen, wild sheep, and parasites along the Mackenzie River ecotone represents a natural model or field laboratory to examine these processes. Additionally, lungworms, *Protostrongylus* spp., had not been reported in muskoxen, and a new geographic record for this nematode was established in Dall's sheep from the northern Richardson Mountains, NT.

**KEY WORDS:** *Protostrongylus stilesi*, muskoxen, Dall's sheep, ecological isolation, colonization, biodiversity survey, Northwest Territories, Yukon Territory, Canada.

Knowledge of the diversity and biogeography of lungworm faunas (Protostrongylidae) among northern species of Bovidae has dramatically increased with a series of recent studies (Hoberg et al., 1995; Kutz, Hoberg, and Polley, 2001; Kutz, Veitch et al., 2001). Among Caprinae, including Dall's sheep *Ovis dalli* Nelson, 1884, and muskoxen *Ovibos moschatus* (Zimmermann, 1780), at high latitudes across the Nearctic, this nematode fauna appears to be characterized by limited diversity. A few species, however, may be widely distributed, and current records have served to establish recognition of a broad geographic range

for *Protostrongylus stilesi* Dikmans, 1931, in the western Nearctic among populations of *O. dalli* in the Subarctic and Arctic and in bighorn sheep *Ovis canadensis* Shaw, 1804, at boreal latitudes (see Kutz, Veitch et al., 2001).

In contrast to the protostrongyle fauna in wild sheep, lungworms are uncommon parasites in both native and introduced populations of muskoxen throughout their current range in the Holarctic (Alendal and Helle, 1983; Hoberg et al., 1995). On the mainland of North America, 2 subspecies of muskoxen are now present (Fig. 1): (1) the native *O. moschatus moschatus* (Zimmermann, 1780), which has a distribution across the central Canadian Arctic; and (2) the introduced

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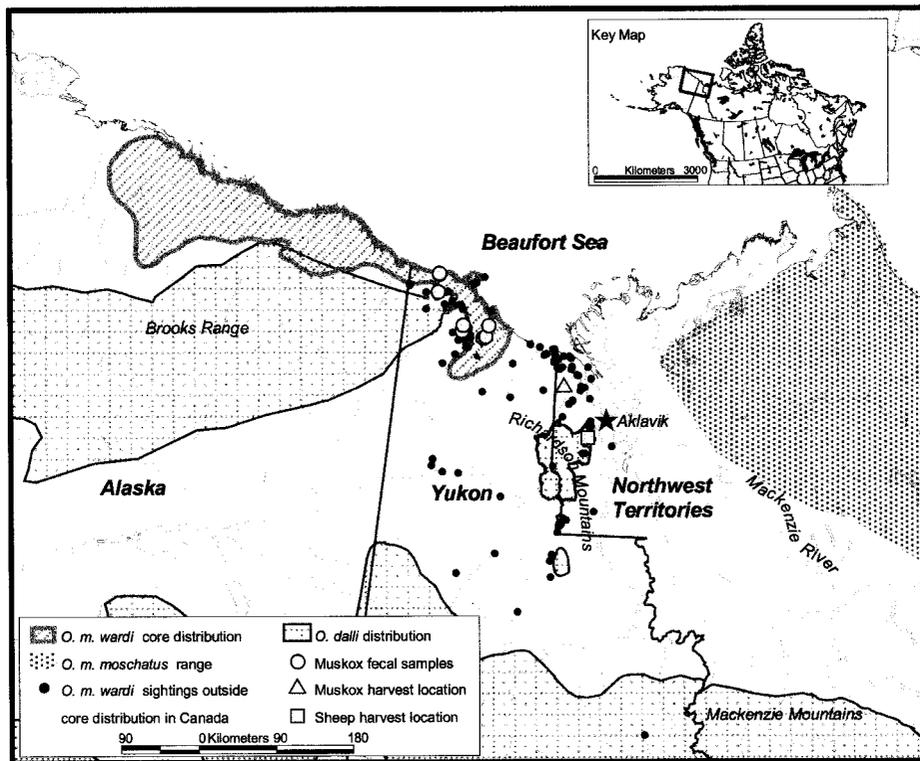


Figure 1. Geographic distributions of populations of muskoxen, including *Ovibos moschatus wardi* and *O. moschatus moschatus*, and Dall's sheep *Ovis dalli dalli*, along with localities of parasitological collections from the Northwest Territories and Yukon Territory, Canada.

*O. moschatus wardi* Lydeker, 1900, which originated by sequential translocation of muskoxen from East Greenland to Nunivak Island, Alaska and subsequently to the Arctic Coastal Plain (Lent, 1999); recruitment on the Arctic Coastal Plain has been accompanied by a rapid range expansion eastward into northwestern Canada over the past decade (Reynolds, 1998). Among these muskoxen in North America, only *Umingmakstrongylus pallikuukensis* Hoberg, Polley, Gunn, and Nishi, 1995, is a characteristic component of the pulmonary helminth fauna and occurs in populations of *O. moschatus moschatus* on the mainland of the central Canadian Arctic (Hoberg et al., 1995; Kutz, 2000; Kutz, Hoberg, and Polley, 2001). Notably, there are no records of larvae or adults attributable to species of *Protostrongylus* Kamensky, 1905, in muskoxen throughout their Holarctic range (Boev, 1975; Alendal and Helle, 1983).

Documentation of the diversity of the northern protostrongylid fauna has often been ham-

pered by the paucity of collections of adult nematodes that are required for definitive diagnosis (Kutz, Veitch et al., 2001) and lack of an ecosystem approach to survey and inventory, which can define the array of species that may circulate among sympatric bovid and cervid hosts (see also Brooks and Hoberg, 2000; Hoberg et al., 2001).

As a component of biodiversity assessment, we report results of surveys documenting distribution, identity, and new records for *Protostrongylus* sp. in *O. moschatus wardi* from the Yukon Territory (YT) and Northwest Territories (NT), Canada. Ecological context for the broader distribution of *Protostrongylus* sp. was gained through concurrent collections of Dall's sheep *O. dalli dalli* Nelson, 1884, from the Richardson Mountains, NT. These data provide a basis for exploring the role and influence of ecological isolation and host switching on parasite faunal diversity among muskoxen, Dall's sheep, and other ruminants in the Arctic. Additionally, we

examine the potential for interchange of parasites between expanding populations of introduced *O. moschatus wardi* and native *O. moschatus moschatus*.

### Materials and Methods

Studies designed to understand biodiversity and the interaction among protostrongylids and northern bovids were based on initial analyses of fecal samples. These were followed by strategic collections of hosts to determine the identity and distribution of parasites (e.g., Kutz, 2000; Kutz, Veitch et al., 2001).

#### Collections from muskoxen

Fecal specimens were collected in April 1999 directly from the recta of 10 adult *O. moschatus wardi* resident in the northwestern YT (in the area 68°58'28.92"N; 138°39'45.72"W to 69°35'33.72"N; 140°08'15.72"W), which had been immobilized for placement of radio collars (Fig. 1). Specimens were frozen and subsequently shipped to the Western College of Veterinary Medicine, Saskatoon, Saskatchewan, Canada, for analysis. Protostrongylid larvae were recovered by standard techniques by use of the beaker-Baermann method (Forrester and Lankester, 1997). Data from these analyses are reported as larvae per gram (LPG) of feces.

On 22 January 2000, 2 adult females and 3 calves near 9 mo of age from the Arctic Coastal Plain near Big Fish River, northwest of Aklavik, NT (ca. 68°33'33.6"N; 136°14'40.5"W), were harvested during a community hunt (Fig. 1). Necropsies were conducted in the field, with lungs frozen and transported to the laboratory at Inuvik, NT for detailed examination for lungworms. Fecal specimens taken at the time of collection revealed the adult muskoxen, but not calves, to have patent infections of protostrongylids, as indicated by first-stage larvae (L1s) of *Protostrongylus* sp. and unidentified dorsal-spined larvae (DSLs). Consequently, calves were not studied in detail, and examinations focused on the female muskoxen specifically for collection of adult lungworms, following procedures outlined by Kutz, Veitch, et al. (2001). Specimens of adult *Protostrongylus* sp. were dissected from the pulmonary parenchyma, preserved in 70% ethanol and 5% glycerine, and later studied under differential interference contrast (Zeiss) as whole mounts cleared in phenol-alcohol or lacto-phenol.

#### Collections from Dall's sheep

We requested hunters in Aklavik, NT to collect and submit lungs, gastrointestinal tracts, and fecal samples from sheep harvested in the local area. Samples were later submitted from 3 sheep taken at Jurassic Butte in the northern Richardson Mountains (ca. 68°01'16.1"N; 135°29'35.8"W), southeast of Aklavik on 19 January 2000 (Fig. 1). The official place name is Jurassic Butte, and the local name is Black Mountain.

#### Specimens examined

The identity of specimens in *O. moschatus wardi* and Dall's sheep was confirmed on the basis of com-

parison to the type series and vouchers of *P. stilesi* in the U.S. National Parasite Collection (USNPC), at the Parasite Biology, Epidemiology and Systematics Laboratory, Animal and Natural Resources Institute, Agricultural Research Service, USDA, Beltsville, Maryland, U.S.A.: (1) USNPC 29379 (types) and 75440 (from the original series) in bighorn sheep *Ovis canadensis* from Colorado, U.S.A.; (2) USNPC 45157 (vouchers) in *O. canadensis* from Jasper, Alberta, Canada; (3) USNPC 45160 in the mountain goat *Oreamnos americanus* (de Blainville, 1816), from Jasper, Alberta; (4) USNPC 49227 in *O. canadensis* from Wyoming, U.S.A.; (5) USNPC 86940 in *O. dalli dalli* from the Mackenzie Mountains, Northwest Territories; and (6) USNPC 90718 (University of Alaska Museum, UAFM 3580, 127, and 128), in *O. dalli dalli* from Dry Creek, Denali, Alaska, U.S.A. Additionally, we examined the types of *Protostrongylus frosti* Honess, 1942, USNPC 36852, in *O. canadensis* from Wyoming.

### Results

Adult specimens of lungworms in 2 adult female muskoxen from the Arctic Coastal Plain and 3 Dall's sheep from the northern Richardson Mountains near Aklavik, NT (Fig. 1), were identified as *P. stilesi*. Voucher specimens were deposited in the USNPC as nos. 90715 and 90716 from *O. moschatus wardi* and 90717, 90813, and 90814 from *O. dalli*.

Nematodes in *O. moschatus wardi* and *O. dalli* were largely identical and were consistent with a series of known specimens including the types and those in *O. dalli* from the Alaska Range and the Mackenzie Mountains (Table 1). Male and female specimens were also in agreement with available descriptions, particularly with respect to the structure of the gubernaculum, including the complex capitulum and laterally expanded distal crura, and in the form of the provagina (Dikmans, 1931, 1943, 1957; Honess, 1942; Zdzitowiecki and Boev, 1971; Monson and Post, 1972). The gubernaculum unequivocally distinguishes *P. stilesi* from those species, *Protostrongylus davtiani* (Savina, 1940), *P. frosti*, *Protostrongylus raillieti* (Schulz, Orloff, and Kutass, 1933), and *Protostrongylus rushi* Dikmans, 1937, which, because of the biogeographic history of the Beringian region or host association, could be present in wild bovids from Alaska.

Measurements of most diagnostic characters were within the ranges previously established for this species. Relative to the original description and subsequent redescrptions, specimens in both *O. moschatus wardi* and *O. dalli* collected adjacent to Aklavik had slightly larger spicules, a

**Table 1. Morphometric data for adult males and females of *Protostrongylus stilesi* in muskoxen, *Ovibos moschatus wardi*, from the Arctic Coastal Plain and Dall's sheep, *Ovis dalli dalli*, from the Richardson Mountains; values in micrometers unless specified otherwise; (n) with range followed by mean  $\pm$  1 SD in parentheses.**

	Musk oxen	Dall's sheep
<b>Males</b>		
Number	20	25
Body length (mm)	(2) 17.55–20.35	(2) 20.28–20.79
Body width	(4) 109–120	(2) 79
Esophagus length	(6) 244–299 (263 $\pm$ 20.51)	(6) 239–271 (263 $\pm$ 13.32)
Esophagus width (base)	(6) 36–47 (40.7 $\pm$ 5.08)	(6) 26–31 (29 $\pm$ 1.78)
Esophagus % body length	1.3–1.4	1.25–1.35
Nerve ring*	—	—
Excretory pore*	(4) 140–286 (201 $\pm$ 63.29)	(6) 273–309 (294 $\pm$ 13.77)
Cervical papillae*	(4) 148–267 (201 $\pm$ 50.82)	(6) 286–307 (299 $\pm$ 7.54)
Left spicule length	(14) 312–390 (367 $\pm$ 21.39)	(21) 330–434 (373 $\pm$ 26.92)
Right spicule	(15) 299–397 (363 $\pm$ 26.82)	(21) 325–437 (371 $\pm$ 28.87)
Gubernaculum length†	(14) 169–227 (210 $\pm$ 17.66)	(21) 175–231 (206 $\pm$ 13.96)
Corpus length‡	(14) 91–137 (120 $\pm$ 14.36)	(21) 94–130 (112 $\pm$ 11.02)
Crura length	(16) 78–104 (90 $\pm$ 5.99)	(21) 81–101 (94 $\pm$ 5.25)
Sickle-plate length	(10) 20–31 (24 $\pm$ 4.19)	(18) 18–26 (21 $\pm$ 2.3)
Ventral plate (telamon)	(12) 78–118 (97 $\pm$ 13.09)	(20) 88–120 (98 $\pm$ 8.26)
<b>Females</b>		
Number	3 partial	2 partial
Total length	—	—
Tail length	(3) 74–77	(2) 94–101
Vulva to anus	(3) 163–204	(2) 179–252
Vulva to tail	(3) 237–281	(2) 273–353
Provaginal length	(2) 125–177	(2) 143–208
Vagina length	(3) 370–459	(2) 322–536
Sphincter length	(3) 56–82	(2) 65–104
Egg length	(10) 89–140 (101 $\pm$ 14.3)	(5) 96–114 (103 $\pm$ 7.4)
Egg width	(10) 44–62 (53 $\pm$ 5.3)	(5) 39–65 (47 $\pm$ 9.4)

\* Distance from anterior extremity.

† Total length, including crura and entire corpus.

‡ Includes distal cuticularized portion and proximal clear portion.

consistently smaller gubernaculum, and larger eggs (Boev, 1975; Kutz, Veitch et al., 2001) (Table 1). There were no apparent differences in the proportions of the corpus or crura in material from *O. canadensis* and that in the present study. Spicule length for specimens in either muskoxen (using the left spicule as representative:  $\bar{x}$  = 367  $\pm$  21.4  $\mu$ m) from the Arctic Coastal Plain or Dall's sheep ( $\bar{x}$  = 373  $\pm$  26.9) from the northern Richardson Mountains, was significantly greater (one-way ANOVA,  $F$  = 36.029,  $P$  < 0.0001) than that observed in populations of *P. stilesi* in Dall's sheep from the Alaska Range (Dry Creek, Denali) ( $\bar{x}$  = 292  $\pm$  1.33  $\mu$ m) or in the Mackenzie Mountains ( $\bar{x}$  = 299  $\pm$  8.1).

Typical L1s of *Protostrongylus* found in Dall's sheep and muskoxen from the NT and YT were morphologically similar ( $\bar{x}$  = 368  $\pm$  22  $\mu$ m in total length for 10 L1s in muskoxen) and were

considered to represent *P. stilesi*; these were also consistent with specimens in Dall's sheep from the Mackenzie Mountains ( $\bar{x}$  = 364  $\pm$  10  $\mu$ m in total length for 10 L1s) (Kutz, Veitch et al., 2001). Near Aklavik, larval protostrongylids were found in both adult female muskoxen and included low numbers of *P. stilesi* (4–10 LPG) and DSLs (~4–5 LPG); larvae were not demonstrated in calves at ~9 mo of age. In the YT, fecal samples from 10 adult muskoxen all contained L1s presumed to be *P. stilesi* (4–78 LPG,  $\bar{x}$  = 33) and DSLs (2–69 LPG,  $\bar{x}$  = 16). The identity of the DSLs was undetermined, although they were morphologically inconsistent with DSLs of *Umingmakstrongylus* (cf. Hoberg et al., 1995).

All adult nematodes were found in the parenchyma, and lesions associated with *P. stilesi* in adult muskoxen were located in the caudodorsal

and diaphragmatic surface of the diaphragmatic lobes. The lesions were tan to red-brown, round to oval, ~3–5 mm in diameter, extended into the pulmonary parenchyma, and contained adult nematodes, eggs, and larvae. Adult parasites were confined to the alveolar parenchyma and were surrounded by a mild to focally marked cellular infiltrate consisting primarily of lymphocytes and a few macrophages (T. Bollinger, unpublished observations). Gross lesions in the lungs of muskoxen and Dall's sheep from both the Richardson and Mackenzie mountains were similar (Kutz, Veitch et al., 2001).

### Discussion

During the current study, specimens of *P. stilesi* were found for the first time in a population of introduced muskoxen (*O. moschatus wardi*) from YT and NT and in Dall's sheep from the Richardson Mountains, NT. Parasites in sympatric muskoxen and Dall's sheep were morphologically indistinguishable, which suggests that they represent a single population distributed between these caprine hosts. The occurrence of *P. stilesi* in muskoxen has both basic and applied significance, serves as a basis for discussion of host specificity and host switching, and has some management implications for parasites in muskoxen.

#### A context for Protostrongylidae and *Protostrongylus* in musk oxen

Prior to the current study, there have been no records of larvae or adults attributable to species of *Protostrongylus* in muskoxen. Although lungworms (Protostrongylidae) are uncommon parasites in *O. moschatus*, sampling effort has been sufficient to demonstrate the occurrence of a number of protostrongylids in muskoxen across the Holarctic. *Umingmakstrongylus pallikuukensis* Hoberg, Polley, Gunn, and Nishi, 1995, is the only characteristic component of the pulmonary helminth fauna in *O. moschatus moschatus* (Hoberg et al., 1995; Kutz, Hoberg, and Polley, 2001). Elsewhere in the Nearctic, DSLs of protostrongylids, distinct from those of *U. pallikuukensis*, were observed during the present study in *O. moschatus wardi* and sporadically in fecal collections from native *O. moschatus moschatus* at mainland localities across the west-central Canadian Arctic (S. J. Kutz, unpublished data). Among *O. moschatus wardi* introduced from East Greenland to Alaska, DSLs presumed

to be a species of *Muellerius* Cameron, 1927, were reported on Nunivak Island (Dau, 1981); the identification is now considered to be in error (Kutz, Veitch et al., 2001). Additionally, in muskoxen that were introduced from Greenland to Scandinavia, DSLs may represent species of *Varestrongylus* Bhaelerao, 1932, or *Elaphostrongylus* Cameron, 1931, acquired from cervids or protostrongylids such as *Cystocaulus* Schulz, Orlov, and Kutass, 1933, that are typical in domestic sheep *Ovis aries* Linnaeus, 1758 (Alendal and Helle, 1983; Holt et al., 1990; Stéen et al., 1994).

Notably, *Protostrongylus* sp. or *P. stilesi* has not been observed in East Greenland or in any populations of *O. moschatus wardi* that have been established from this or related sources—e.g., Norway; Svalbard, Sweden; Nunivak Island, Alaska; and the Taimyr Peninsula, Russia (Bos, 1967; reviewed in Allendal and Helle, 1983; Hoberg et al., 1995). Thus, the occurrence of *P. stilesi*, otherwise a parasite characteristic of *Ovis* spp. in the Nearctic, is not linked to translocation of previously infected muskoxen from Nunivak Island to the Arctic Coastal Plain (for a history of translocations and introductions, see Lent, 1999).

#### Range and morphological variation of *P. stilesi* in Dall's sheep

A new geographic record and identification of this protostrongylid from the Richardson Mountains implies a broad distribution for *P. stilesi* in *O. dalli* (Kutz, Veitch et al., 2001). First stage larvae, presumed to be *P. stilesi*, have been found in Dall's sheep from the central Alaska Range (Goble and Murie, 1942), the Brooks Range, the Mackenzie Mountains, and the Richardson Mountains (Kutz, Veitch et al., 2001). There have been few definitive identifications, and only recently have records been published of adult *P. stilesi* from localities in Alaska (Dry Creek, near Denali) and NT (Mackenzie Mountains) (Kutz, Veitch et al., 2001).

Among Dall's sheep, hosts and parasites appear to occupy a series of disjunct ranges, and as such may be indicated by morphological variation for some characters in *P. stilesi*. Discrete variation in spicule length was observed between *P. stilesi* in muskoxen on the Arctic Coastal Plain and Dall's sheep from the Richardson Mountains, and in sheep from the Mackenzie Mountains and Alaska Range, on the ba-

sis of comparisons during the present study. This may be consistent with highly isolated populations of *P. stilesi* in Dall's sheep, a history of range fragmentation, and limited contemporary gene flow for parasites and hosts. Comparisons of these putative populations and an evaluation of this hypothesis are currently being conducted on the basis of molecular analyses.

#### ***P. stilesi* in muskoxen and Dall's sheep**

As has been documented above, *P. stilesi*, a typical lungworm in wild thin-horned sheep at Arctic and Subarctic latitudes in the Nearctic (Kutz, Veitch et al., 2001), had not been reported previously in *O. moschatus*. It cannot be excluded, however, that other species of *Protostrongylus* could be present in Alaska, NT, and YT. On the basis of the present study, protostrongylids, including *P. stilesi*, appear to be common and widespread in *O. moschatus wardi* from YT and western NT; the protostrongylid fauna in muskoxen from Alaska is unknown. Additionally, *P. stilesi* does not appear to be present in *O. moschatus moschatus* from eastern and central NT and Nunavut, on the basis of extensive examinations of lungs and fecal samples that have been conducted in surveys for *U. pallik-uukensis* (e.g., Hoberg et al., 1995; Kutz, 2000; Kutz, Hoberg and Polley, 2001).

The occurrence of *P. stilesi* in a population of introduced muskoxen is indicative of a contemporary colonization event from Dall's sheep. The morphological uniformity of specimens from the Arctic Coastal Plain and the Richardson Mountains is consistent with this contention but would not refute the possibility of an already broader distribution for *P. stilesi* in muskoxen north of the Brooks Range in Alaska. On the basis of the documented distribution of protostrongylids in members of Caprini and *Ovibos* (Boev, 1975; Alendal and Helle, 1983; Hoberg et al., 1995; Carreno and Hoberg, 1999; Kutz, 2000), however, it is evident that *Protostrongylus* was not derived from Nunivak Island or from East Greenland with the original translocation of *O. moschatus wardi*.

Data are compatible with acquisition of *P. stilesi* by muskoxen in contact with thin-horned sheep, which are the typical and well-established hosts in YT, NT, and Alaska. Such host switching could have accompanied the contact among muskoxen and Dall's sheep in the Brooks Range after their initial introduction to the Arctic

Coastal Plain or may be a more recent event coincidental with contact in the region of the Richardson Mountains (Fig. 1). Strategic collections in Alaska to establish the identity of *Protostrongylus* sp. in Dall's sheep and any potential occurrence in *O. moschatus wardi* are necessary to evaluate these alternative hypotheses regarding distribution.

#### **Host specificity, host switching, and ecological isolation for *P. stilesi***

Host specificity has both historical/phylogenetic and ecological/contingent components, and the interaction of these determinants influences the ultimate host distribution of a given parasite species (e.g., Poulin, 1998). Interestingly, muskoxen appear to acquire parasites when in sympatry with source populations of bovid or cervid hosts (reviewed by Alendal and Helle, 1983), which suggests that, for *O. moschatus*, the barriers to infection by helminths may be primarily ecological, as opposed to physiological (see also Lent, 1999). Ecological isolating mechanisms may constitute the basis for limitations in host distribution for some parasites, which indicates that narrow host specificity can be contextual. The observed distribution of *P. stilesi* in wild sheep (e.g., in bighorn sheep *O. canadensis* and thin-horned sheep *O. dalli* ssp.) (Becklund and Senger, 1967) and, less often, mountain goats *Oreamnos americanus* (Boddicker et al., 1971), across its range in the Nearctic may indicate a level of specificity that is more apparent than real. Thus, the potential for host switching among some bovids could be limited currently by isolation and habitat segregation. Such may be consistent with reports of this protostrongylid in *O. americanus* when it is in contact with *O. canadensis* (Boddicker et al., 1971).

In a contemporary context, colonization of muskoxen by parasites may be a predictable event in zones of sympatry with Dall's sheep (Fig. 1). The core distribution for *O. moschatus wardi* on the Arctic Coastal Plain is, to some degree, parapatric to that of *O. dalli* in the eastern Brooks Range and areas of the Richardson Mountains. Radio-collared muskoxen, which are known to be infected with *Protostrongylus*, appear to be in sympatry, or at a minimum seasonally occupy common range, with Dall's sheep in this region (Fig. 1). It appears probable that muskoxen are exposed to infection during the summer, when herds move into higher coun-

try to escape insects and occupy the winter ranges of Dall's sheep. Maintenance of sympatry in zones of contact may be critical for host switching from Dall's sheep to muskoxen, but it is not known whether viable populations and transmission of *P. stilesi* can be maintained in the absence of *O. dalli*. Notably, the distribution of *P. stilesi* in muskoxen in the YT and NT (Fig. 1) suggests that this bovid could be a mediator for dispersal and, thus, gene flow among otherwise isolated populations of parasites in Dall's sheep from the eastern Brooks Range and northern Richardson Mountains.

In a historical context, during the Pleistocene, sympatry within an assemblage of large ungulates, including wild sheep and muskoxen, was probably more extensive than it is at present (Guthrie, 1982, 1984; Vereshchagin and Baryshnikov, 1982). The existence of a Pleistocene megafauna, characterized by extensive sympatry and high diversity, indicates the potential for colonization by parasites among ecologically similar hosts (Hoberg et al., 1995, 1999). Climatological fluctuations and habitat perturbation at the termination of the Pleistocene led to range restriction and diminished sympatry and may have been a contributing factor in extinction for some species of the mammalian community. A pattern of increasing allopatry during the Holocene may have been a driver for alteration in structure for parasite faunas: (1) lower parasite faunal diversity in some host groups, (2) post-glacial isolation, as a determinant of divergence in parasite populations; and (3) apparent specificity for some parasites that is currently maintained by altitudinal or latitudinal restrictions on the ranges of contemporary populations of ungulates. These factors reinforce recognition of the role of ecological isolating mechanisms as determinants of the distribution and historical and contemporary structure of parasite faunas in northern ruminants (Hoberg et al., 1999).

Disruption of contemporary ecological isolating barriers can result from habitat perturbation, either anthropogenically or climatologically driven, and from management practices that influence the distribution of ungulate hosts (Hoberg, 1997; Daszak et al., 2000). Climate change may drive habitat alteration that leads to shifting distributions, range expansion, and more extensive seasonal overlap among species that are segregated by seasonal effects, altitude, or latitude—i.e., the concept of a breakdown in iso-

lating mechanisms and the generation of interfaces that drive host switching (Hoberg, 1997). Consequently, if zones of contact become more extensive or the temporal limit on allopatry is relaxed, we may observe increasing instances of host switching by parasites or pathogens at the interface of newly emerging ecotones. Such a prediction relates to apparent specificity that is maintained ecologically for a diversity of helminth parasites. For example, both *P. stilesi* in musk oxen, which is derived from contact with *O. dalli*, and the abomasal nematode *Ostertagia gruehneri* Skrjabin, 1929, in Dall's sheep (E. P. Hoberg, S. J. Kutz, and A. Veitch, unpublished data), derived from caribou *Rangifer tarandus* (Linnaeus, 1758), would be in this category (Hoberg et al., 2001).

#### Parasites in introduced and native muskoxen

The recent expansion of the populations of *O. moschatus wardi* on the mainland, which has resulted in range overlap with Dall's sheep in the Richardson Mountains, is also expected to lead to new contact zones for native and introduced muskoxen that could further influence parasite distribution. Muskoxen (i.e., *O. moschatus wardi*) originally introduced to Alaska from East Greenland have rapidly occupied habitat on the Arctic Coastal Plain (Reynolds, 1998; Lent, 1999), with an eastward range expansion that now includes the Richardson and northern Mackenzie mountains and the outer Mackenzie River Delta (Veitch et al., 2000; J. Nagy, unpublished observations) (Fig. 1). Concurrently, native muskoxen (i.e., *O. moschatus moschatus*) from the population on the east-central mainland of NT have been dispersing westward from their core range (Veitch, 1997; Fournier and Gunn, 1998). It is currently unknown whether these populations have developed a contact zone, although their distributions may now be limited by the Mackenzie River.

As has been documented in the current study, *P. stilesi* is a common parasite in *O. moschatus wardi*, at a minimum across a limited zone in the northern Richardson Mountains and on the eastern region of the Arctic Coastal Plain (Fig. 1) but is unknown in *O. moschatus moschatus*. In contrast, *U. pallikuukensis* is prevalent in *O. moschatus moschatus*, has a distribution currently limited to the region east of the Mackenzie River, and has not been observed in *O. mos-*

*chatus wardi* (Kutz, 2000; Kutz, Hoberg, and Polley, 2001). Consequently, there are management implications with respect to the potential for exchange of protostrongylids as well as other macro- and microparasites between these expanding populations (Hoberg, 1997), given the apparent nature of ecological controls on the distribution of helminths in muskoxen.

Alteration in complex host-parasite systems in the north that may be linked to climatologically and anthropogenically driven global change and the effects of management must be tracked within the context of biodiversity survey and inventory and programs to develop archival collections as the foundation for monitoring ecosystem-level perturbations (Brooks and Hoberg, 2000). The current developing interface for native and introduced muskoxen, wild sheep, and parasites along the Mackenzie River ecotone represents a potential natural model and field laboratory in which to explore the interaction of parasites and naive host populations in the prevailing regime of environmental change. Practical benefits are gained in defining the role of parasites and parasitism as factors that influence population health among northern ruminants. Such unique systems also constitute meaningful baselines for examining dynamic interfaces for host-parasite assemblages and a means to elucidate critical data for understanding the primary limiting factors that control parasite distribution, transmission, faunal structure, and patterns of emerging disease (Hoberg, 1997; Brooks and Hoberg, 2000).

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