# THE BIOLOGY OF THE GASTRO-INTESTINAL HELMINTHS OF WOODLAND AND BARREN-GROUND CARIBOU (*Rangifer tarandus*)

BY

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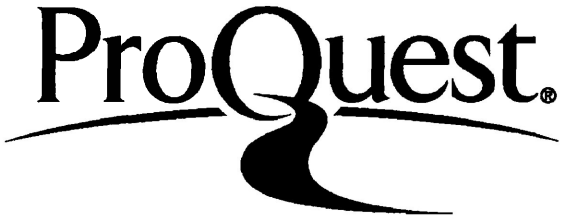

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## ABSTRACT

Twenty-one species of helminths were recovered from wild and captive caribou (*Rangifer tarandus*). Woodland caribou of the Slate Islands, barren-ground caribou of the Beverly herd and captive woodland caribou were parasitized by 7, 7 and 16 species of gastro-intestinal helminths respectively. The predominant nematode recovered from all wild caribou was *Ostertagia gruhneri.* The lung worm, *Dictyocaulus viviparus*, was recovered from both wild and captive woodland caribou. The large number of species recovered from captive caribou suggested that cross transmission of parasites between captive caribou and a variety of other ungulates was common.

*Ostertagia gruhneri* appears to be a polymorphic species with *O. arctica* representing its minor form. The minor form never comprises more than 10% of the total number of male *Ostertagia*, has stout, heeled spicules and Sjoberg's organ. The wide spread occurrence of polymorphism among the Ostertagiinae suggests that a re-evaluation of the characters used to define genera and species is required.

The average number of adult abomasal nematodes (3247) recovered from caribou of the Slate Islands was higher than reported for other wild cervids in North America. The number of abomasal nematodes present in animals was related to herd density. Adult worms were more numerous during the spring and fall (x=4370) than in the winter (x=1280). Inhibited fourth-stage *O. gruhneri* were found in wild caribou from the Slate Islands and comprised up to 85% of the total worm burden during the winter. No apparent disease caused by any helminth was observed in wild caribou. Captive caribou subjected to various forms of stress developed heavy infections of abomasal nematodes (>20000) which appear to have been partially responsible for the death of two animals.

Seasonal fluctuations in the number of nematode eggs passed in the feces of

wild and captive caribou were evident. Fecal egg counts from Slate, Pic and Otter Islands and captive adult caribou were similar during the spring and summer. Peak egg counts were observed in wild and captive animals during the fall. The low number of *Ostertagia* sp. eggs passed in the feces of caribou during the winter months is due to the presence of fewer, less fecund worms.

The free-living stages of *Nematodirella* spp. were more resistant to freezing and dessication than those of *Ostertagia* spp.. Eggs of *Nematodirella* frozen for 11 months or more hatched, while those of *Ostertagia* would not hatch after freezing for 1 day. Infective larvae of *Nematodirella longissimespiculata* also appeared to withstand freezing and dessication better than those of *Ostertagia* spp.

Caribou appear to develop a well marked immunity to nematodes of the genera *Nematodirella, Nematodirus* and *Dictyocaulus.* Calves are usually the only animals infected. Immunity to *O. gruhneri* was also evident. Worms recovered from caribou calves of the Slate Islands were longer and more fecund than those recovered from adults at the same location. The relationship between host age, herd density and worm morphology suggested that woodland caribou of Pic Island are not as heavily parasitized as caribou from the Slate Islands. Stresses of the rut, injury or relocation appear to compromise acquired immunity to gastro-intestinal nematodes.

Anthelmintic treatment of captive caribou with Ivomec eliminated patent infections of *Ostertagia* spp., *Trichuris* sp., *Capillaria* sp. and *Oesophagostomum venulosum.* Ivomec was not effective against *Nematodirus* sp.. Treatment appeared to be effective against inhibited larvae of abomasal nematodes. Ivomec may be useful as a prophylactic measure when transferring wild caribou.

Wild moose (*Alces alces*) from northwestern Ontario were parasitized by two species of gastro-intestinal helminths. Ninety-six percent of moose examined were infected with *Nematodirella alcidis.* The average number of worms recovered from

wild moose was 111, considerably lower than recorded in caribou. The majority of worms recovered in most infections were immature. This appears to be the first report of inhibited fourth-stage *N. alcidis*. Abomasal nematodes were not recovered from wild moose of northwestern Ontario.

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# INTRODUCTION

The importance of parasitic disease as a mortality factor in caribou and reindeer (*Rangifer tarandus*) is not well understood (Miller 1982). Instances of neurological disease caused by the nematode, *Elaphostrongylus cervi* in Newfoundland (Lankester and Northcott 1979) and bronchopneumonia caused by infections of *Dictyocaulus viviparus* in association with *Pasteurella multocida* in Norway (Kummeneje 1977) are known. Bacterial and viral agents are also known to cause disease in caribou and reindeer (Dieterich 1980; Kummeneje 1980; Thing and Clausen 1980). Despite numerous studies of the gastro-intestinal helminths of caribou and reindeer, their effects and potential to cause disease are not well known (Kummeneje 1980; Dieterich 1980; Miller 1982).

Abomasal nematodes are known pathogens of domestic animals in temperate regions (Gibbs 1982). Naturally occurring disease caused by *Haemonchus contortus* (Prestwood and Kellogg 1971) and *Ostertagia ostertagi* (Conti and Howerth 1987) have been reported in white-tailed deer of the United States. Rehbinder and von Szokolay (1978) investigated the possible role of abomasal nematodes as a cause of winter mortality of Swedish reindeer calves. No evidence that these worms were responsible for mortality was observed. Prior to this study, caribou calves held in captivity occasionally demonstrated diarrhoea during the late fall (Lankester unpublished). Such signs have been associated with heavy infections of abomasal nematodes (Dunn 1978).

Caribou calves are known to suffer high mortality during their first few months (Miller 1982). Mortality may be caused by severe weather, poor nutrition of calf or cow and predation. Periodic outbreaks of high caribou calf

mortality have been noted in areas where caribou exist in large numbers and have had an impact on their environment (Thing and Clausen 1980, Clausen et al. 1980). Young animals are generally thought to be more susceptible to disease than older animals (Gibbs 1973). However, the role of gastro-intestinal helminths as a factor affecting the survival of caribou calves is unknown.

High ungulate densities are known to favour the transmission and acquisition of large numbers of abomasal nematodes (Eve and Kellogg 1977). At present, woodland caribou (*R. t. caribou*) persist as scattered herds along the north shore of Lake Superior. These herds may occasionally attain high densities when confined to islands in the absence of predators. The Slate Islands herd presently exists at the highest caribou density known in North America (Bergerud 1985). Historically, the Slate Islands herd has undergone large fluctuations in population size (Anon. 1986). Winter severity and the availability of food undoubtedly limit population increase. The importance of parasitic disease in causing winter mortality that periodically reduces the herd to low numbers is unknown. One might predict that caribou existing at high densities such as those found on the Slate Islands, would tend to carry heavier worm burdens than low density herds and thus be more susceptible to outbreaks of disease.

Recently, the Ontario Ministry of Natural resources made an effort to rehabilitate caribou in areas where they once thrived. The presence of a high density herd of caribou on the Slate Islands provides a readily available source of stock for such projects. Because of the lack of knowledge concerning the potential hazards posed by the introduction of parasites with their hosts, studies on anthelmintics were conducted to determine their efficacy against parasites of caribou.

The presence of a high density herd of wild caribou on the Slate Islands and the availability of a captive herd provided the opportunity to determine the possible role of gastro-intestinal helminths in causing disease. The aim of the present study was to examine the life history dynamics and potential pathogenicity of parasites in insular herds of woodland caribou of Northwestern Ontario. Initial efforts were concerned with the identification of species parasitizing caribou, with special emphasis on possible differences between calves and adults. Seasonal studies on the biology of the gastro-intestinal helminths parasitizing caribou were conducted on wild and captive animals.

Samples from barren-ground caribou of the Beverly herd, Northwest Territories, and from woodland caribou herds in northwestern Ontario and Newfoundland were also examined. Similar studies were conducted on wild and captive moose of Northwestern Ontario.

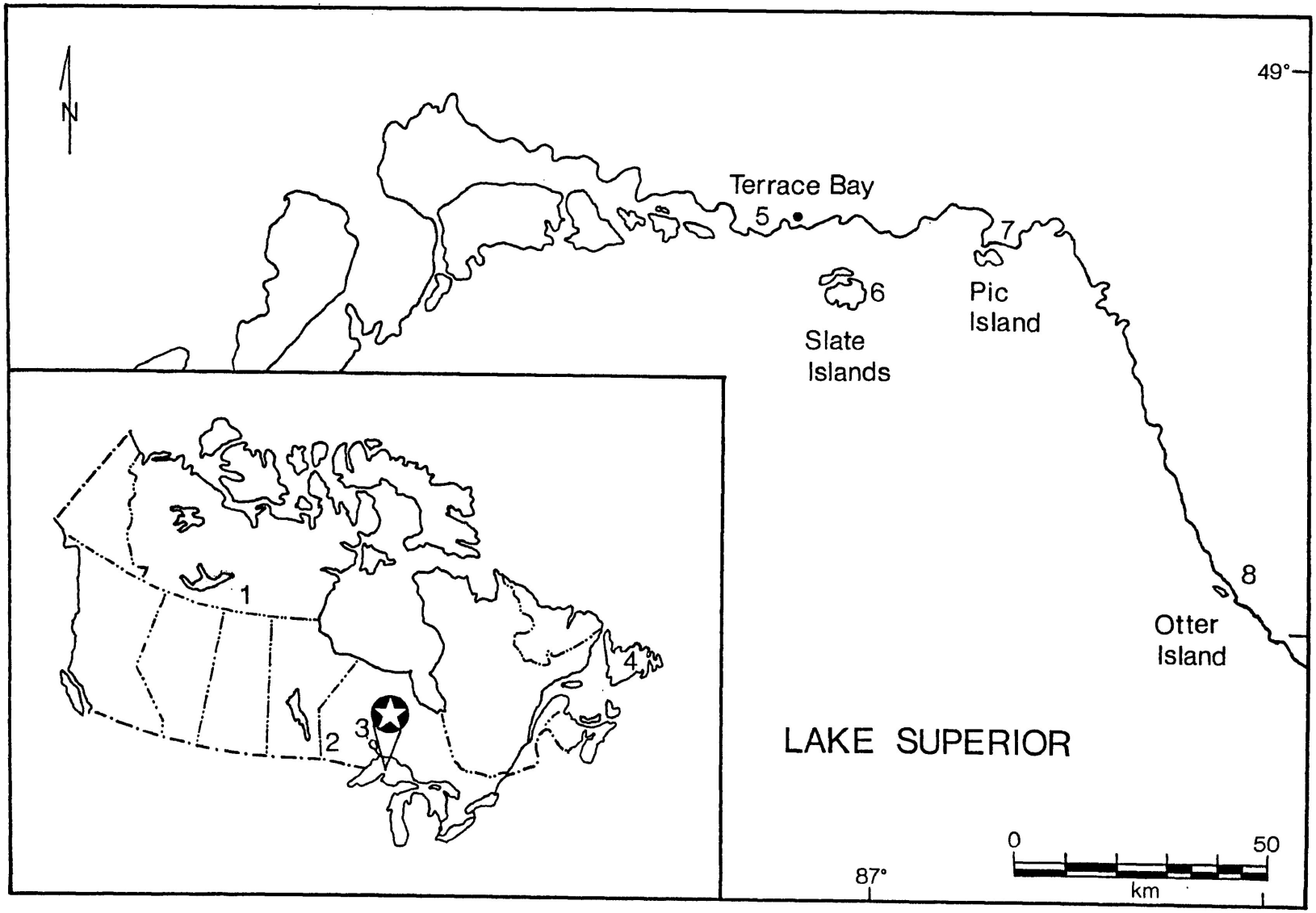
## MATERIALS AND METHODS

*Caribou sampled*

Both woodland caribou (*Rangifer tarandus caribou*) and barren-ground caribou (*R. t. groenlandicus*) were examined for gastro-intestinal helminths. Samples from woodland caribou in northwestern Ontario were from animals on the Slate Islands in Lake Superior (84°40' N, 87°00' W), on Pic Island and Coldwell Peninsula (48°43' N, 86°37' W), in Pukaskwa National Park including those on Otter Island (48°07' N, 86°04' W), and a small group of animals near Schreiber (48°48' N, 87°15' W) (Fig. 1). Additional samples were collected from woodland caribou near Red Lake (51°00' N, 93°50' W) and Armstrong (50°18' N, 89°02' W).

The Slate Islands consist of five main islands and several smaller islands totaling 36 $km^2$, 13 km off the north shore of Lake Superior near Terrace Bay. During the course of the study, the Slate Islands herd fluctuated between 400 and 600 animals (Bergerud 1985; Anon. 1986). These animals frequently swim between islands but rarely to and from the mainland. The Pic Island herd consists of approximately 50 animals located on a 10.4 $km^2$ island, 1-2 km off the north shore of Lake Superior, near Coldwell Peninsula. These animals are known to frequent Coldwell Peninsula (Ferguson 1982). Samples collected from the few animals present on Coldwell Peninsula were combined with the Pic Island samples. A third herd was studied in Pukaskwa National Park. Approximately 25 caribou are present within the 1878 $km^2$ park (Bergerud 1985); seven of these are on Otter Island (L. Krysyl, personal communication). The island is 2 $km^2$ and located 0.5 km off the north shore of Lake Superior. Up to 25 animals that winter at Armstrong are from the Nipigon herd which

Fig. 1. Map of study areas showing location of caribou herds in Northwestern Ontario (star, enlargement), Newfoundland and the Northwest Territories. (1) Beverly herd, Northwest Territories; (2) Red Lake, Ontario; (3) Armstrong, Ontario; (4) Topsails, Newfoundland; (5) Schreiber; (6) Slate Islands; (7) Pic Island and Coldwell Peninsula; (8) Otter Island and Pukaskwa National Park.


N
49°
Terrace Bay
5
7
6
Pic
Island
Slate
Islands
8
Otter
Island
1
2
3
4
LAKE SUPERIOR
0
50
km
87°

numbers approximately 80-100 animals (Bergerud 1985). Samples were also collected from woodland caribou of the Topsails Herd in central Newfoundland (49°05' N, 56°40' W).

Samples from barren-ground caribou of the Beverly herd were collected 110-150 km northeast of Fort Smith, Northwest Territories (60°00' N, 111°51' W) where the animals winter (Fig. 1). The Beverly herd numbers 94,000 and occupies central Northwest Territories (Miller 1982). In addition, five fecal samples were collected during June, 1986, at the Kettle River, Manitoba (56°55' N, 89°23' W), from a migratory caribou herd occupying the area around James Bay in Manitoba and Ontario.

In addition to the collections from wild animals, a captive herd of woodland caribou originating from the Slate Islands, Ontario and from the Middle Ridge area of central Newfoundland, was maintained at the Kakabeka Falls Game Farm, Kakabeka Falls, Ontario. Captive animals were allowed to roam free on 36 ha of fenced land consisting of open grassy areas mixed with stands of coniferous and deciduous trees. During fall and winter the captive animals were fed alfalfa hay and grain to supplement natural grazing. Other animals sharing range with captive caribou included moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), sika deer (*Cervus nippon*), fallow deer (*Dama dama*), llamas (*Lama glama*), cattle (*Bos taurus*) and horses (*Equs caballus*).

*Collection and identification of helminths*

Material examined from free-ranging caribou consisted of feces, intestinal tracts and lungs. Fecal collections were made monthly from March to October, 1985 on the Slate Islands and whenever possible from the other woodland

caribou herds. Only feces judged to have been deposited during the previous two days were collected. The criteria used to estimate the age of fecal material included color, moistness and absence of beetles and leaf litter on the pellet group. Whenever possible, samples were obtained from animals that were handled live or observed defecating. Samples were placed in plastic bags and kept cool until transported to the laboratory. Complete carcasses or portions thereof were examined from the Slate Islands whenever available.

Fecal material was collected from known-age animals of the Beverly herd during December 1984, March and December 1985 and March and December 1986. Small portions of abomasal contents as well as sections of duodenum were collected from 10 animals during March 1985. The total number of abomasal nematodes present in small, weighed subsamples of abomasal contents was estimated using the mean weight of abomasal contents of captive caribou that died during the course of the study.

Fecal samples were collected weekly from captive caribou and occasionally from the other ungulate species present. In 1985 and 1986, caribou calves born in captivity were examined weekly starting approximately three weeks after birth. Samples from two captive moose were collected on a weekly basis from July 1984 to September 1985. Whenever possible, carcasses of animals from the Kakabeka Falls Game Farm were examined for adult helminths.

All fecal material was stored at 3°C until examined. Differential fecal egg counts were made using a sugar centrifugation flotation technique (Samuel and Trainer 1969). Slides were examined systematically in their entirety for helminth ova at 30-40 X using a compound microscope. Sequential slides from each flotation were examined until the last one added no more than 15% to the total number of eggs. If no eggs were detected on the first slide, a second

was examined in order to ensure that the sample was negative. Trichostrongyloid eggs were counted and the intensity of infection expressed as the number per gram of dried feces (EPG) while the presence of other helminth ova was noted for calculations of prevalence. Weighed samples of feces were oven dried at 50°C in order to correct egg counts for excess fecal moisture caused by seasonal variation in the diet and the presence of snow in winter samples. Differences in parasite prevalence and number of eggs in feces were analyzed in relation to host age using a $X^2$ statistic and F test respectively (Steel and Torrie 1980).

Eggs were identified to species or genus based on their size and morphology following descriptions provided by Dewhirst and Hansen (1961), Samuel and Beaudoin (1965), Samuel and Gray (1974) and Christie and Jackson (1982). Eggs within adult females recovered at necropsy were also used as an aid to identification of ova in feces. Fifty eggs of each type were drawn and measured with the aid of a drawing tube and stage micrometer.

Contents of the abomasum, duodenum and cecum were examined for the presence of adult and immature gastro-intestinal helminths. Contents, and scrapings of the mucosa were washed with running water on a 0.8 mm screen and examined in gridded Petri dishes using a stereo microscope at 6-25 X. All adult nematodes were counted. The total number of inhibited larvae ($L_4$) present in the abomasum was estimated by determining the ratio of $L_4$ to adults, present in small, unscreened subsamples of abomasal contents. Early attempts to recover immature stages by digesting portions of the abomasal wall produced few larvae. Advanced decomposition of the abomasal mucosa may have released larvae into the abomasal contents. The mucosa of the abomasum and duodenum were examined for adult and immature helminths by squashing

between two glass plates. When fragmented worms were encountered, only portions of adults with an intact bursa or ovejector were counted. Sex ratios were determined by counting the number of males and females present in the first 100 worms recovered.

Nematodes were fixed in 10% glycerin in 70% alcohol or in 10% formalin and cleared in lactophenol for identification based on spicule and bursal characteristics of the males. Identification of adult helminths follows the keys of Skrjabin *et al.* (1954), Becklund and Walker (1967a,b), Gibbons and Khalil (1982), Durette-Desset (1983), Knight (1983) and Lichtenfels and Pillet (1983a,b). Original descriptions were used to supplement published keys when needed. Nematodes were drawn and measured with the aid of a drawing tube and stage micrometer.

When possible, the total length of 30 male and 30 female abomasal nematodes was measured from each animal necropsied. The length of spicules was measured in dorsal view. The number of shelled eggs *in utero* (a measure of fecundity) and the presence or absence of a vulval flap was noted for each female. Worm length, spicule length and fecundity were analyzed in relation to host age using an F test (Steel and Torrie 1980). The fecundity of female worms was also analyzed by season. A probability level of $<0.05$ was considered significant for all statistical tests. Mean values reported in text are followed by standard error or range.

Moose carcasses or viscera supplied by hunters were examined during the fall and road kills provided material at other times of the year. A 10% subsample of the abomasal contents and portion of the wall and contents of the duodenum as well as feces were examined for trichostrongyloid nematodes and their ova.

Samples of the abomasal wall were preserved in 10% formalin for histological examination of lesions and histotrophic forms. Tissue was embedded in paraffin, sectioned at 6 to 10 $\mu$m and stained in Lillie's A & B (Lillie 1954).

*Studies of free-living stages.*

Larvae of abomasal nematodes were cultured to the third stage ($L_3$) in moistened feces held at room temperature (19-25°C) and recovered using the Baermann technique. Attempts to culture eggs of *Nematodirella* spp. and *Nematodirus* spp. using this method were unsuccessful. Thereafter, Nematodirid eggs were recovered by flotation and rinsed off coverslips into gridded 25 mm Petri dishes with distilled water to a depth of 2 mm. Development of *Nematodirella longissimespiculata* was monitored at various temperatures from 3°C to 35°C and the date of first and last hatching was noted.

To determine their resistance to freezing, eggs of *Ostertagia* spp. and *Nematodirella longissimespiculata* were held at -18°C in fecal material for various lengths of time. After thawing, eggs were isolated by flotation, incubated in distilled water at 25°C and the number of larvae hatching was noted.

Lots of 10, third-stage larvae of *Ostertagia* spp. and *N. longissimespiculata* from caribou, and *N. alcidis* from moose were tested for their ability to survive freezing, dessication or both. Larvae were dessicated by suspending them in a small drop of distilled water which was allowed to evaporate at room temperature. Larvae were frozen at -18°C in distilled water or after dessicating for one day. Larvae of *Osteragia* and *Nematodirella* were dessicated, frozen, or both for 1, 3, 5, 10, 20, and 30 days then thawed and/or

rehydrated with distilled water, to determine what proportion survived. The number of $L_3$'s motile after 24 h at room temperature was recorded.

An experiment was conducted to determine if chilling prior to freezing affected the survival of infective larvae of *Ostertagia* spp.. Lots of 10 larvae were chilled for 1 day at 3°C prior to freezing for 1, 3, 6, 10 and 20 days. Larvae frozen without prior chilling served as controls.

During the winter of 1986, field temperatures were recorded in air, snow (5cm depth) and at the snow-soil interface at the time of collections from captive animals.

*Anthelmintic studies*

The efficacy of Ivomec (ivermectin, Merck) against gastro-intestinal helminths of caribou was studied. Animals were given a subcutaneous injection at 0.2 mg/kg estimated body weight. Animals were treated in February (n=1), April (n=7), July (n=1), September (n=4), October (n=1) and November (n=1). Feces from animals treated in September were collected daily for three days following treatment to determine how quickly egg numbers declined. Treatments were considered successful if eggs were absent in the feces when animals were examined one week later.

## RESULTS

*Helminth species recovered from wild and captive caribou*

A total of 21 species of helminths was recovered from wild and captive caribou. These included nine species in woodland caribou of the Slate Islands, seven from barren-ground caribou of the Beverly herd (Table 1) and 17 in captive caribou (Table 2). Examination of carcasses of other ungulate species sharing range with captive caribou revealed the presence of three species not recovered in caribou (Table 2).

Additional data on the distribution of helminths in woodland caribou of northwestern Ontario and Newfoundland were obtained from fecal flotations. Trichostrongylid ova (probably *Ostertagia* spp.) were present in the feces of caribou from all herds examined (Pic Island, Pukaskwa, Schreiber, Red Lake, Nipigon and Topsails). Ova of *Nematodirella longissimespiculata* were recovered in the feces from Pukaskwa, Nipigon and Topsails animals. The presence of *Nematodirus odocoilei* in the Topsails herd was indicated by typical ova in the feces. *Capillaria* sp. and *Monezia* sp. were present in most herds. Ova of *Trichuris* sp. were detected in the feces of animals from the Pukaskwa and Topsails herds.

*Identification of gastro-intestinal helminths*

*Redescription of Nematodirus tarandi*

*Nematodirus tarandi* Hadwen, 1922 was first described from reindeer (*R. t. tarandus*) in Alaska. Shortly thereafter, Mitskewitch (1929) described *Nematodirus skrjabini* from reindeer in the Soviet Union. Dikmans (1936) recognised the similarity of these species and suggested that *N. skrjabini* was a synonym of *N. tarandi.* Skrjabin et al. (1954) did not agree with this

Table 1. Helminths recovered from wild woodland caribou of the Slate Islands, Ontario, and barren-ground caribou of the Beverly herd, Northwest Territories.

| Species | Herd | | Accession No.[a] |
|---|---|---|---|
| | Slate | Beverly | |
| *Ostertagia gruhneri* | A[b] | A | 79039 (S)[c] |
| *Ostertagia arctica* | A | A | 79258 (S) |
| *Teladorsagia circumcincta* | 0[d] | A | 79471 (B) |
| *Nematodirella longissimespiculata* | A,E | A,E | 78611 (S) |
| *Nematodirus tarandi* | 0 | A,E | 79038 (B) |
| *Monezia* sp. | E | E | |
| *Capillaria* sp. | E | 0 | |
| *Trichuris* sp. | E | 0 | |
| *Skrjabinema* sp. | A | A | |
| *Dictyocaulus viviparus* | A | 0 | 79358 (S) |
| *Setaria yehi* | A | | 79588 (S) |

[a] Accession numbers of voucher specimens deposited in the United States National Museum, Helminth collection.

[b] Identifications based on adult worms recovered at necropsy (A) or by typical eggs in feces (E).

[c] Indicates whether specimens are from the Slate Islands (S) or Beverly (B) herd.

[d] 0 indicates that the species was not found at necropsy or in feces.

Table 2. Gastro-intestinal helminths recovered from captive woodland caribou (Car), moose (Mo), white-tailed deer (WTD), fallow deer (FD), sika deer (SD), llamas (LL) and cattle (C) at the Kakabeka Falls Game Farm.

| Parasite | Host | | | | | | | Acc. no.[a] |
|---|---|---|---|---|---|---|---|---|
| | Car (5)[b] | Mo (1) | WTD (0) | FD (0) | SD (2) | LL (0) | C (1) | |
| Trichostrongylid ova | E[c] | E | E | E | 0[d] | E | E | |
| *Ostertagia gruhneri* | A | 0 | | | 0 | | 0 | 79039 |
| *Osteragia arctica* | A | 0 | | | 0 | | 0 | 79258 |
| *Ostertagia ostertagi* | A | A | | | 0 | | A | 79267 |
| *Ostertagia leptospicularis* | A | A | | | 0 | | 0 | 79596 |
| *Ostertagia kolchida* | A | 0 | | | 0 | | 0 | 79271 |
| *Spiculopteragia assymmetrica* | A | 0 | | | 0 | | 0 | 79467 |
| *Spiculopteragia spiculoptera* | A | 0 | | | 0 | | 0 | 79468 |
| *Nematodirella longissimespiculata* | A,E | 0 | 0 | 0 | 0 | 0 | 0 | 78611 |
| *Nematodirus odocoilei* | A,E | E | 0 | 0 | 0 | 0 | 0 | 78609 |
| *Nematodirus helvetianus* | A,E | 0 | 0 | 0 | 0 | 0 | 0 | 79472 |
| *Cooperia punctata* | 0 | 0 | | | 0 | | A | 79270 |
| *Cooperia oncophora* | 0 | 0 | | | 0 | | A | 79269 |
| *Trichostrongylus axei* | A | A | | | 0 | | A | 79268 |
| *Trichostrongylus vitrinus* | A | 0 | | | 0 | | 0 | 79469 |
| *Haemonchus contortus* | 0 | A | | | 0 | | 0 | 79470 |
| *Oesophagostomum venulosum* | A,E | E | E | E | A,E | E | 0 | 79359 |
| *Capillaria* sp. | A,E | E | E | 0 | 0 | 0 | 0 | - |
| *Trichuris ovis* | A,E | E | 0 | 0 | 0 | 0 | 0 | 79360 |
| *Dictyocaulus viviparus* | A | A | - | - | 0 | - | - | 79358 |
| *Monezia* sp. | E | E | 0 | 0 | 0 | 0 | 0 | |

[a] Voucher specimens deposited in United States National Museum, Helminth collection.

[b] Number in brackets indicates the number of animals necropsied.

[c] Species diagnosed by adults at necropsy (A) or typical eggs in feces (E)

[d] 0 indicates that species was not found at necropsy,or indicated by typical ova in fecal samples; - indicates that appropriate organ was not examined or species can not be distinguished by eggs.

synonymy and argued that *tarandi* was a representative of the genus *Nematodirella.* In an effort to determine the proper generic status of *N. tarandi*, the type specimens (United States National Museum (USNM), Helminth Collection, No. 24611, 1 male, 1 female), paratypes (USNM Helm. Coll. No. 24960, 3 males, 3 females) and topotypes (USNM Helm. Coll. No. 26169.03, 6 males, 6 females) were examined. Hadwen's specimens were compared with those collected in this study from caribou of the Beverly Herd, Northwest Territories and with the original description of *N. skrjabini* (Mitskewitch 1929).

All specimens examined in the present study (Hadwen's and Beverly) possessed similar synlophe, spicules and ova. The body length of type specimens and paratypes was shorter than recorded from worms recovered from the Beverly herd. Spicule tips of *N. skrjabini* drawn by Mitskewich (1929) were identical to those of *N. tarandi.*

*Nematodirus tarandi* is redescribed and drawings are provided. The range of measurements reported is based on the original material collected by Hadwen (1922b) and from specimens collected during this study from barren-ground caribou in the Northwest Territories.

Male: Length 11.4 to 20.45 mm (Table 3). Synlophe consisting of 42 longitudinal cuticular ridges in the region of the excretory pore and cervical papillae (Fig. 2c); 38-52 near mid-body. Dorsal cuticular ridges absent at the level of the proximal end of the spicules. Head vesicle present, 120-160 $\mu$m long with transverse striations. Corona radiata with 42-52 teeth (Fig 2a). Dorsal esophageal tooth present in anterior end of esophagus; visible in lateral view of cleared specimens. Esophagus 680 to 750 $\mu$m long. Excretory pore at the level of the posterior end of esophagus.

Table 3. Comparison of measurements of *Nematodirus tarandi* and *Nematodirus skrjabini*.

| | *N. tarandi* | | | | | |
|---|---|---|---|---|---|---|
| | Hadwen[a] | Types (24611)[b] | Paratypes (24960) | Topotypes (26169.03) | This study (79039) | *N. skrjabini*[c] |
| n | | 1 | 3 | 6 | 10 | - |
| Male (length)[d] | 12.0 | 13.2 | 12.72 (11.4-14.8) | 16.03 (14.65-18.0) | 18.75 (16.75-20.45) | 15.5-17.25 |
| Spicule (length) | 2.72 | 1.32 | 1.46 (1.38-1.51) | 1.5 (1.37-1.6) | 1.45 (1.39-1.51) | 1.4-1.5 |
| Female (length) | 16.0 | 18.3 | 18.3 (16.5-19.0) | 20.7 (17.35-24.65) | 24.1 (21.65-28.7) | 28.55-29.46 |
| Vulva[e] | | 10.8 | 10.5 (10.05-11.0) | 11.45 (9.7-14.5) | 13.8 (11.45-15.1) | 10.88-11.16 |
| Egg length | 75-100 | | 175-215 | 210-220 | 186-220 | 220-265 |
| width | 50-75 | - | 90-105 | 95-100 | 92-108 | 84-114 |

[a] Measurements from original description by Hadwen (1922b).

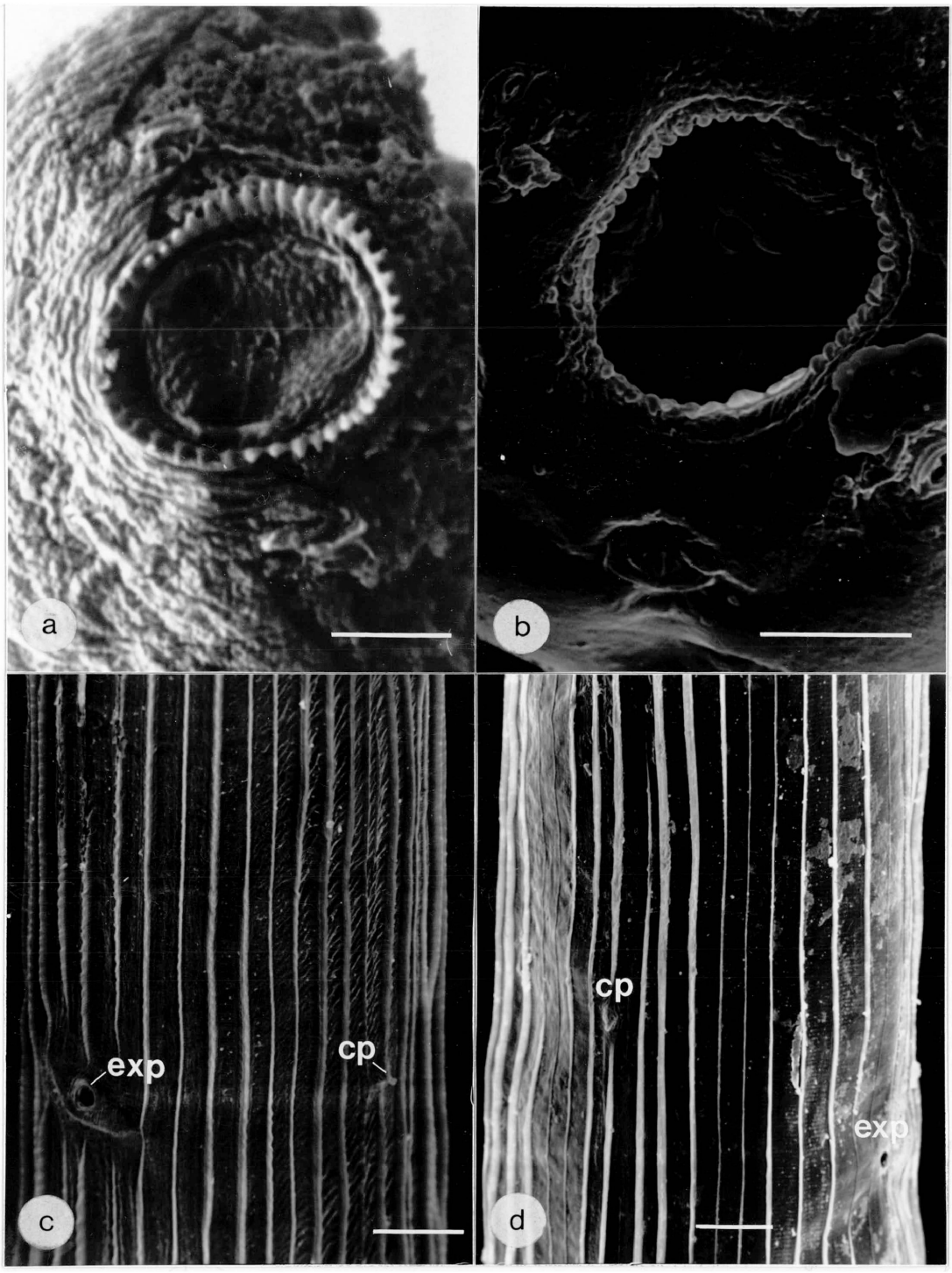
[b] United States National Museum, Helminth Collection Accession Numbers.

[c] Measurements from original description by Mitskewich (1929) (*in* Skrjabin et al. 1954).

[d] All measurements are in mm except eggs which are μm.

[e] Distance from anterior end except *N. skrjabini* which is from posterior end.

Fig. 2. Scanning electron micrographs of en face view (a,b) and synlophe (c,d) in region of excretory pore (ep) and cervical papillae (cp) of *Nematodirus* recovered from caribou. (a,c) *Nematodirus tarandi. (b,d) Nematodirus odocoilei.* Scale bars = 5 $\mu$m (a,b) and 10 $\mu$m (c,d).


a
b
exp
cp
c
cp
exp
d

Bursa with a large number of bosses; rays typical of the genus (Fig. 6d). Dorsal ray paired, bifurcated in distal one sixth of its length. Spicules 1.32 to 1.60 mm long, joined in distal 60% by a clear membrane. Distal end of spicule tips fused, terminating in a distinct, foot-like process flexed ventrally at heel in distal 53-65 $\mu$m (Fig. 6c).

Female: Length 16.5 to 28.7 mm (Table 3). Synlophe as in male, absent posterior to the vulva. Vulva in posterior half of body, 52 to 62% of body length from anterior end. Both arms of reproductive tract functional. Eggs 85 to 105 $\mu$m wide by 185 to 228 $\mu$m long, typically passed in the eight cell stage. Tail of female ends in a terminal spine.

Keys to Trichostrongyloidea in North American caribou and moose

Male abomasal nematodes were identified using characteristics of the bursa, spicules and synlophe (longitudinal cuticular ridges). The three genera of Ostertagiinae can readily be distinguished by the arrangement of the bursal rays (Durette-Desset 1982) and the shape of the dorsal ray (Fig. 3). Bursal types referred to in this key follow the terminology of Durette-Desset (1982) and refer to groupings of the terminal portions of rays 2-6. Species of *Ostertagia, Teladorsagia,* and *Spiculopteragia* were best separated by the morphology of the spicule tips and the accessory bursal membrane. *Trichostrongylus* spp. lack cuticular ridges, are generally small and have a well developed gubernaculum. Males of the Nematodirinae possess spicules longer than 0.5 mm, have a distinct cephalic vesicle and a bursa with paired, bifurcate dorsal rays. Species of Nematodirinae were distinguished by the size

and shape of the spicules and the presence or absence of bosses on the bursa.

**Key to species of male Trichostrongyloidea parasitizing caribou and moose of North America** (Adapted in part from Lichtenfels and Pilitt 1983 a,b and Durette-Desset 1983).

1a Spicules > 0.5 mm long. Dorsal ray paired and bifurcated at its tip (Figs. 6,7). Cephalic vesicle prominent. Parasites of the small intestine. ..... Nematodirinae .. 2

1b Spicules < 0.5 mm long. Dorsal ray not paired (Fig. 3). Cephalic vesicle inconspicuous. Parasites of the abomasum and intestine. ..... 5

2a Spicules > 5 mm long. Few bursal bosses (Fig. 6b). ..... ..... *Nematodirella* spp... 3

2b Spicules < 2 mm long. Bursal bosses numerous (Fig. 6d, 7b,d). ..... *Nematodirus* spp... 4

3a Parasites of caribou. From 44-52 cuticular ridges at the base of the esophagus. ..... *N. longissimespiculata* (Fig. 6a,b)

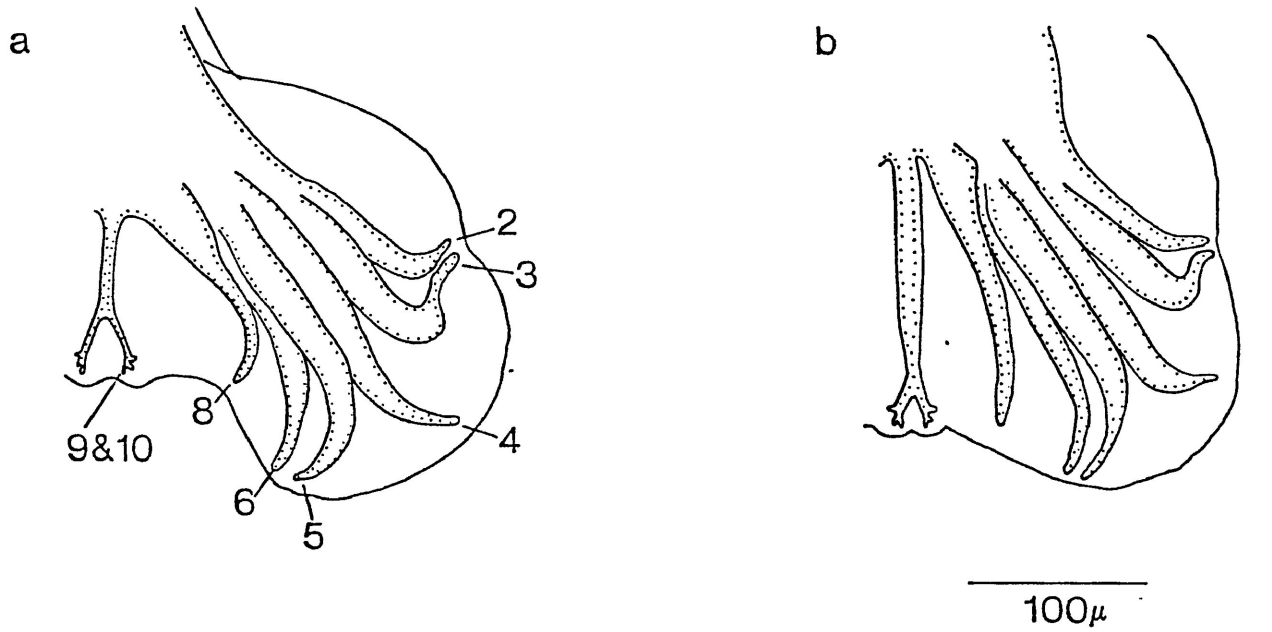
3b Parasites of moose. From 28-34 cuticular ridges at the base of the esophagus. ..... *N. alcidis*

4a Spicules 1.3 to 1.6 mm long, terminating in a foot-like process. From 38-42 cuticular ridges at the base of the esophagus. ..... ..... *N. tarandi* (Fig. 6c,d 2,c)

4b Spicules end in simple point (Fig. 7a). Twenty-six cuticular ridges at the base of the esophagus. ..... *N. helvetianus*

4c Spicules with small lateral processes near distal end (Fig. 7c). From 38-46 cuticular ridges near base of esophagus. .....

Fig. 3. Dorso-lateral view of right half of bursa of Ostertagiinae in caribou. (a) *Ostertagia gruhneri*; (b) *Ostertagia kolchida*; (c) *Teladorsagia circumcincta*; (d) *Spiculoteragia spiculoptera*. System of bursal ray numbering follows that of Durette-Desset (1983). Rays 0, 1 and 7 are not visible in drawings.


a
2
3
8
9&10
4
6
5
b
100μ

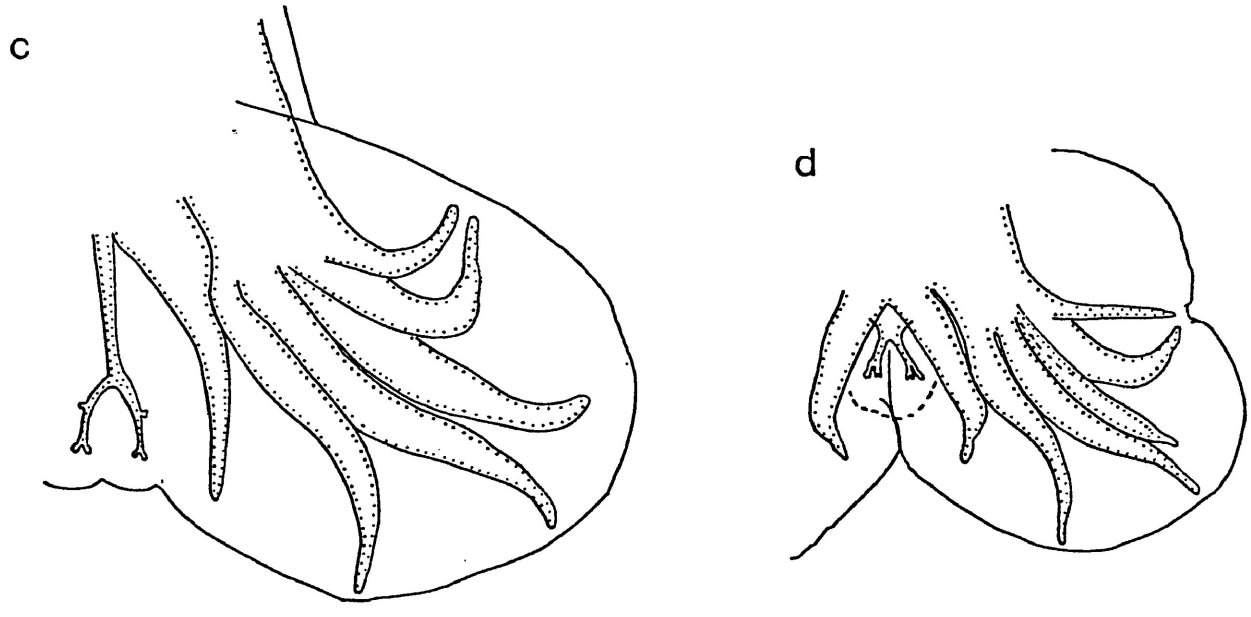

c
d

Fig. 4. Dorsal (on left) and externo-lateral (on right) views of distal end of right spicule of Ostertagiinae in caribou. (a) *Ostertagia gruhneri*; (b) *Teladorsagia circumcincta*; (c) *Ostertagia leptospicularis*; (d) *Ostertagia ostertagi*; (e) *Ostertagia kolchida*; (f) *Ostertagia arctica.*

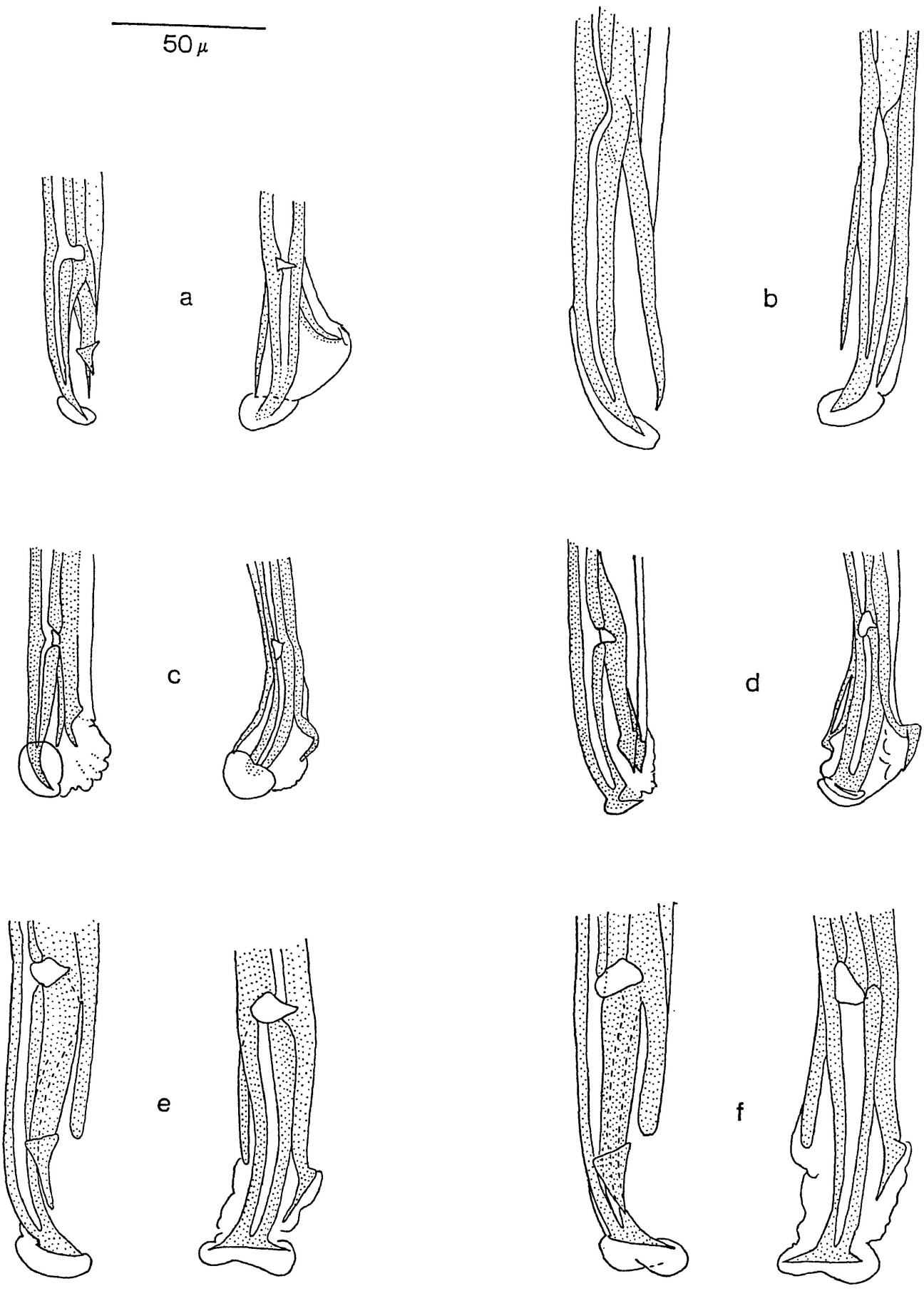

50 μ
a
b
c
d
e
f

Fig. 5. Dorsal view of accessory bursal membrane (a-d,g) and Sjoberg's organ (e,f) of Ostertagiinae recovered in caribou. (a) *Ostertagia gruhneri*; (b) *Teladorsagia circumcincta*; (c) *Ostertagia leptospicularis*; (d) *Ostertagia ostertagi*; (e) *Ostertagia arctica*; (f) *Ostertagia kolchida*; (g) *Spiculopteragia spiculopterta.*

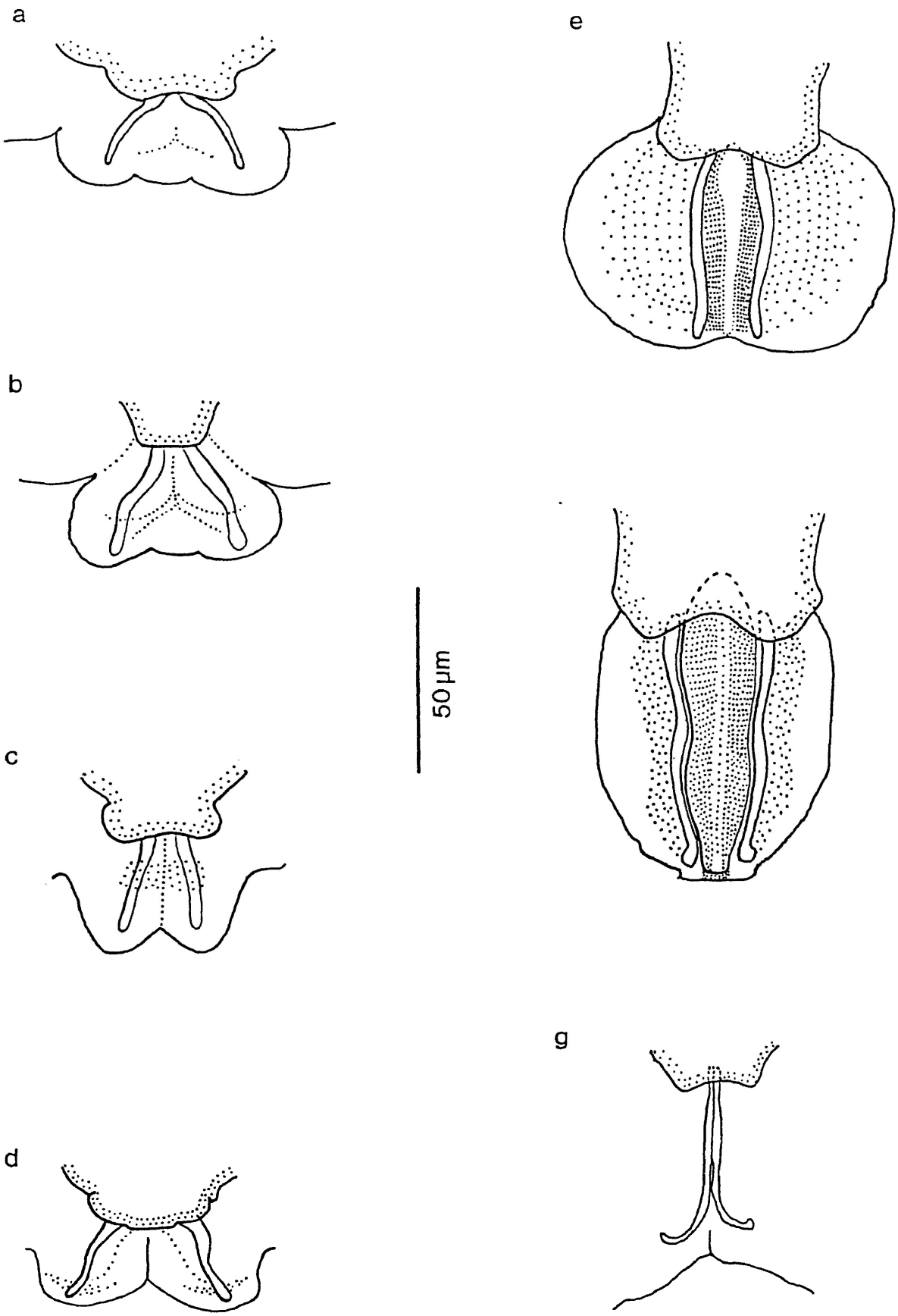
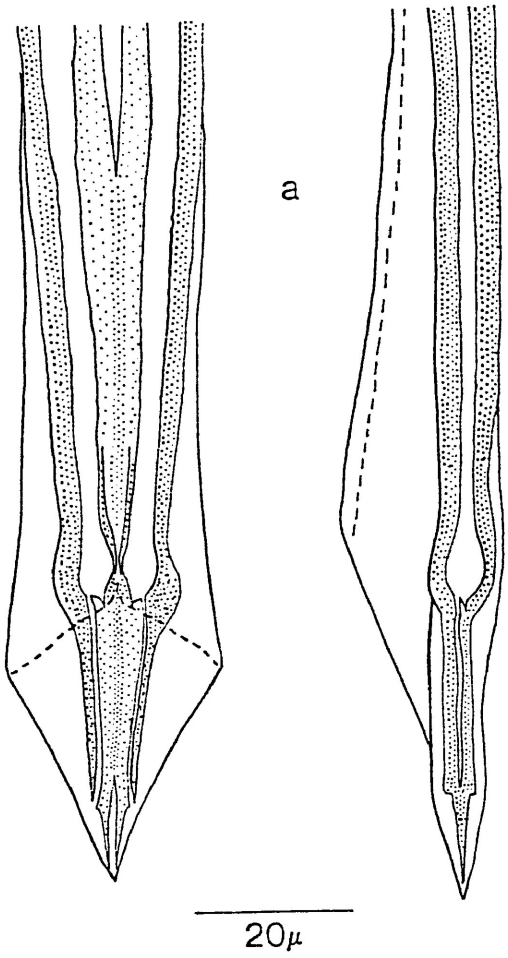
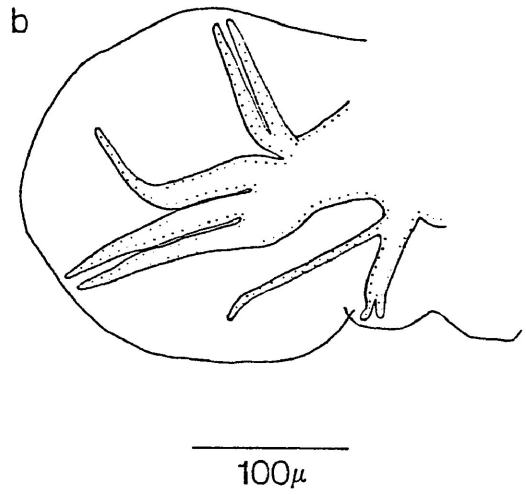
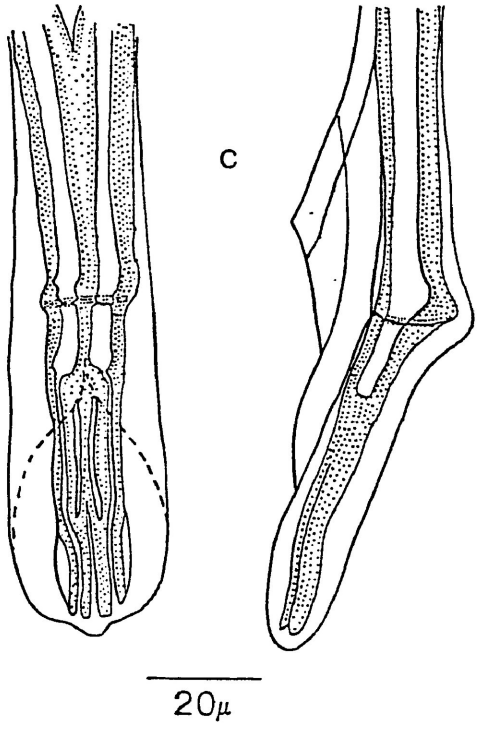

a
b
c
d
e
g
50 µm

Fig. 6. Spicule tips (dorsal view on left and left–lateral view on right) and dorso-lateral view of left half of bursa of Nematodirinae parasitizing wild caribou. (a,b) *Nematodirella longissimespiculata*; (c,d) *Nematodirus tarandi.*


a
20μ


b
100μ


c
20μ

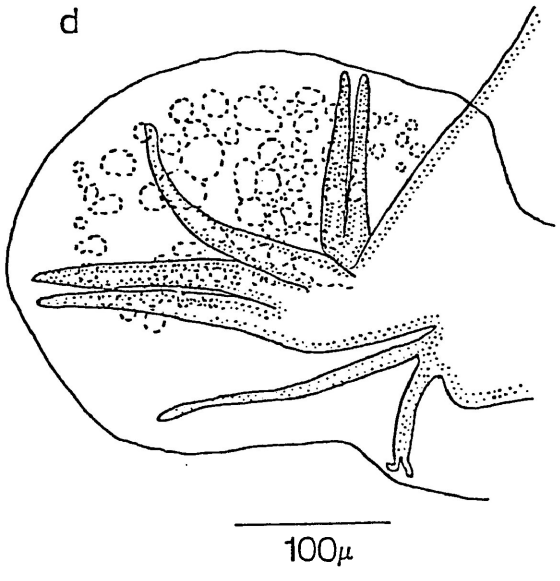
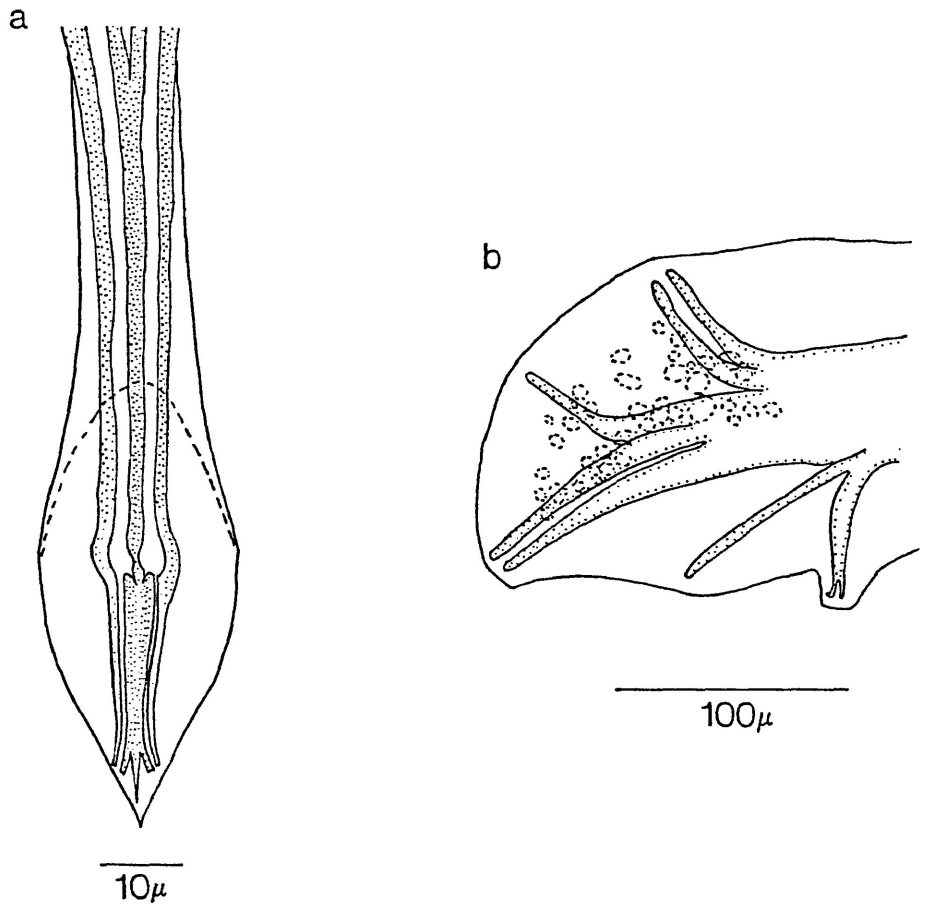

d
100μ

Fig. 7. Dorsal view of spicule tip and dorso-lateral view of left half of bursa of Nematodirinae in captive caribou. (a,b) *Nematodirus helvetianus*; (c,d) *Nematodirus odocoilei.*


a
10μ
b
100μ
c
10μ
d
100μ

..... *N. odocoilei* (Fig. 7c,d) (Fig. 2,d)

5a Cuticular ridges absent. ..... *Trichostrongylus* spp. .. 6

5b Cuticular ridges present..... Ostertagiinae .. 7

6a Spicules unequal in length. Parasites of the abomasum..... *T. axei*

6b Spicules similar in length. Parasites of the duodenum..... *T. vitrinus*

7a Bursa type 2-1-2 (Fig. 3a,b)..... *Ostertagia spp.*.. 8

7b Bursa type 2-2-1 (Fig. 3c,d)..... 11

8a Spicules thin (Fig. 4a,c,d). Accessory bursal membrane delicate with divergent rays (Fig. 5a-d). Dorsal ray < 35% of bursal length (measured from papillae 1 to end of bursa) ..... 9

8b Spicules thick, main trunk with pointed heel (Fig. 4e,f). Accessory bursal membrane with prominent thickening between rays (Sjoberg's organ) (Fig. 5e,f). Dorsal ray > 45% of bursal length..... 10

9a Both dorsal and ventral processes of spicule end in a barb, tip of spicule blunt (Fig. 4d)..... *O. ostertagi*

9b Dorsal process of spicule longer than ventral process, tip of spicule with sharp point (Fig. 4a)..... *O. gruhneri*

9c Dorsal process of spicule equal in length to ventral process. Tip of spicule with large, round cap (Fig. 4c)..... *O. leptospicularis*

10a Sjoberg's organ wider than long (Fig. 5e). Found in association with *O. gruhneri*. ..... *O. arctica*

10b Sjoberg's organ longer than wide (Fig. 5f). Found in association with *O. leptospicularis*. ..... *O. kolchida*

11a Spicules terminate in simple points (Fig. 4b). Accessory bursal membrane with divergent rays (Fig. 5b). Ray 4 as long as ray 5 (Fig. 3c)..... ..... *Teladorsagia circumcincta*

11b Spicules with complex tips and fan-like membranes. Accessory bursal membrane with rays parallel along most of their length (Fig. 5g); ray 4 shorter than ray 5 (Fig. 3d). ..... *Spiculopteragia* spp... 12

12a Spicules similar, 170-200 μm long. ..... *S. spiculoptera*

12b Spicules dissimilar, 200-245 μm long. Right spicule with lateral knob in distal quarter. ..... *S. asymmetrica*

Female abomasal nematodes could be distinguished by the shape, orientation and position of the vulva, and the presence or absence of cuticular ridges. Females of the Ostertagiinae have a transverse vulva and prominent cuticular ridges. Female *Trichostrongylus* lack cuticular ridges and have a longitudinal vulva. Female Nematodirinae were distinguished by the size of the eggs in the uterus, position of the vulva and the number and arrangement of the cuticular ridges. Length of ovejector is measured from the proximal margin of each sphincter.

**Key to species of female Trichostrongyloidea parasitizing caribou and moose of North America** (Adapted in part from Lichtenfels and Pilitt 1983 a,b).

1a Cuticular ridges absent. Longitudinal vulva. ..... *Trichostrongylus* spp.

1b Cuticular ridges present. Cephalic vesicle indistinct. ..... Ostertagiinae ..2

1c Cuticular ridges present. Eggs > 145 μm long. Cephalic vesicle prominent. ..... Nematodirinae .. 3

2a Ovejector 280-350 μm long. Cervical papillae large (>14 μm) (Fig. 8a,b). ..... *Ostertagia* spp.

2b Ovejector 600-700 μm long. Cervical papillae large (>15 μm) (Fig. 8c,d). ... ..... *Teladorsagia circumcincta*

2c Ovejector 220-315 μm long. Cervical papillae small (<8 μm) (Fig. 8e,f). .... ..... *Spiculopteragia* spp.

3a Eggs < 230 μm. Vulva in posterior half of body. Both uteri with eggs. ... .....*Nematodirus* spp. ..4

3b Eggs > 230 μm long. Vulva in anterior half of body. Anterior half of reproductive system atrophied. ..... *Nematodirella* spp. ..5

4a From 38-46 cuticular ridges at base of esophagus (Fig 2d). Ridges continuous to within 100 μm of anus. Eggs 145-170 μm long (Fig. 9d). .... ..... *N. odocoilei*

4b From 38-42 cuticular ridges at base of esophagus (Fig. 2c). Cuticular ridges absent in posterior quarter. Eggs 190-230 μm long (Fig. 9e)..... ..... *N. tarandi*

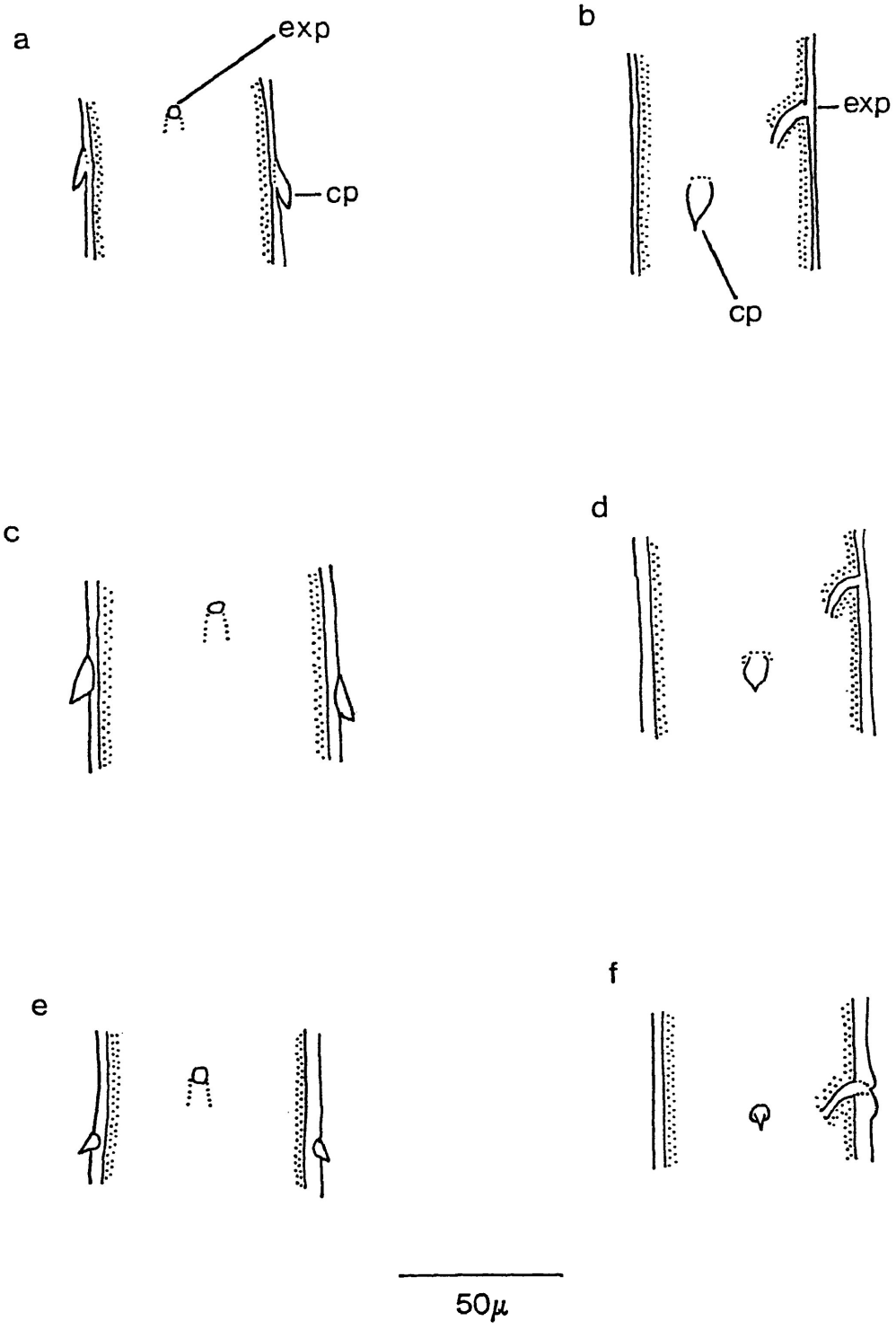
4c Twenty-six cuticular ridges at base of esophagus. ..... *N. helvetianus*

5a More than 40 cuticular ridges in region of excretory pore..... ..... *N. longissimespiculata*

5b Less than 35 cuticular ridges in region of excretory pore. ..... ..... *N. alcidis*

Eggs were distinguished based on shape, length and the presence or absence of polar plugs or a pyriform apparatus (Fig. 9, Table 4). Two types of trichostrongyloid eggs were recovered, those from the abomasal nematodes

Fig. 8. Ventral (a,c,e) and right lateral (b,d,f) view of cervical papillae (cp) and excretory pore (exp) of Ostertagiinae recovered in caribou. (a,b) *Ostertagia gruhneri*; (c,d) *Teladorsagia circumcincta*; (e,f) *Spiculopteragia spiculoptera.*


a
exp
cp
b
exp
cp
c
d
e
f
50μ

(Ostertagiinae and *Trichostrongylus*) which are small (80-100 μm long) and passed in the morula stage, and those of the Nematodirinae which are large (> 140 μm long) and typically passed in the 8 cell stage (Table 4, Fig. 9).

**Key to ova of gastro-intestinal helminths of caribou and moose of North America.**

1a Eggs with polar plugs. ..... 2

1b Eggs without polar plugs. ..... 3

2a Eggs barrel shaped, 45-55 μm x 25-30 μm. Plugs recessed or level with terminal ends (Fig. 9a). ..... *Capillaria* sp.

2b Eggs oval, 65-70 x 30-35 μm. Polar plugs protruding (Fig. 9b). ..... *Trichuris* sp.

3a Eggs square, containing a pyriform apparatus (Fig. 9c). ..... *Monezia* sp.

3b Eggs without pyriform apparatus. ..... 4

4a Eggs > 140 μm long. ..... Nematodirinae .. 5

4b Eggs < 120 μm long. ..... 7

5a Mean length of eggs > 240 μm (Fig. 9d). ..... *Nematodirella* sp.

5b Eggs < 230 μm in length. ..... *Nematodirus* .. 6

6a Eggs 140-180 x 68-82 μm (Fig. 9e). ..... *N. odocoilei*

6b Eggs 180-228 x 85-108 μm (Fig. 9f). ..... *N. tarandi* or *N. helvetianus*

7a Eggs 72-103 x 39-53 μm. Cells light brown (Fig. 9g). ..... *Ostertagia* spp.

7b Eggs 90-110 x 45-69 μm. Cells dark brown (Fig. 9h). ..... *Oesophagostomum* sp.

Fig. 9. Photomicrographs of gastro-intestinal helminth ova recovered by flotation (Scale bars= 50 $\mu$m). (a) *Capillaria sp.*; (b) *Trichuris ovis*; (c) *Monezia* sp.; (d) *Nematodirus odocoilei*; (e) *Nematodirella longissimespiculata*; (f) *Nematodirus tarandi*; (g) *Ostertagia spp.;* *(h) Oesophagostomum venulosum.*

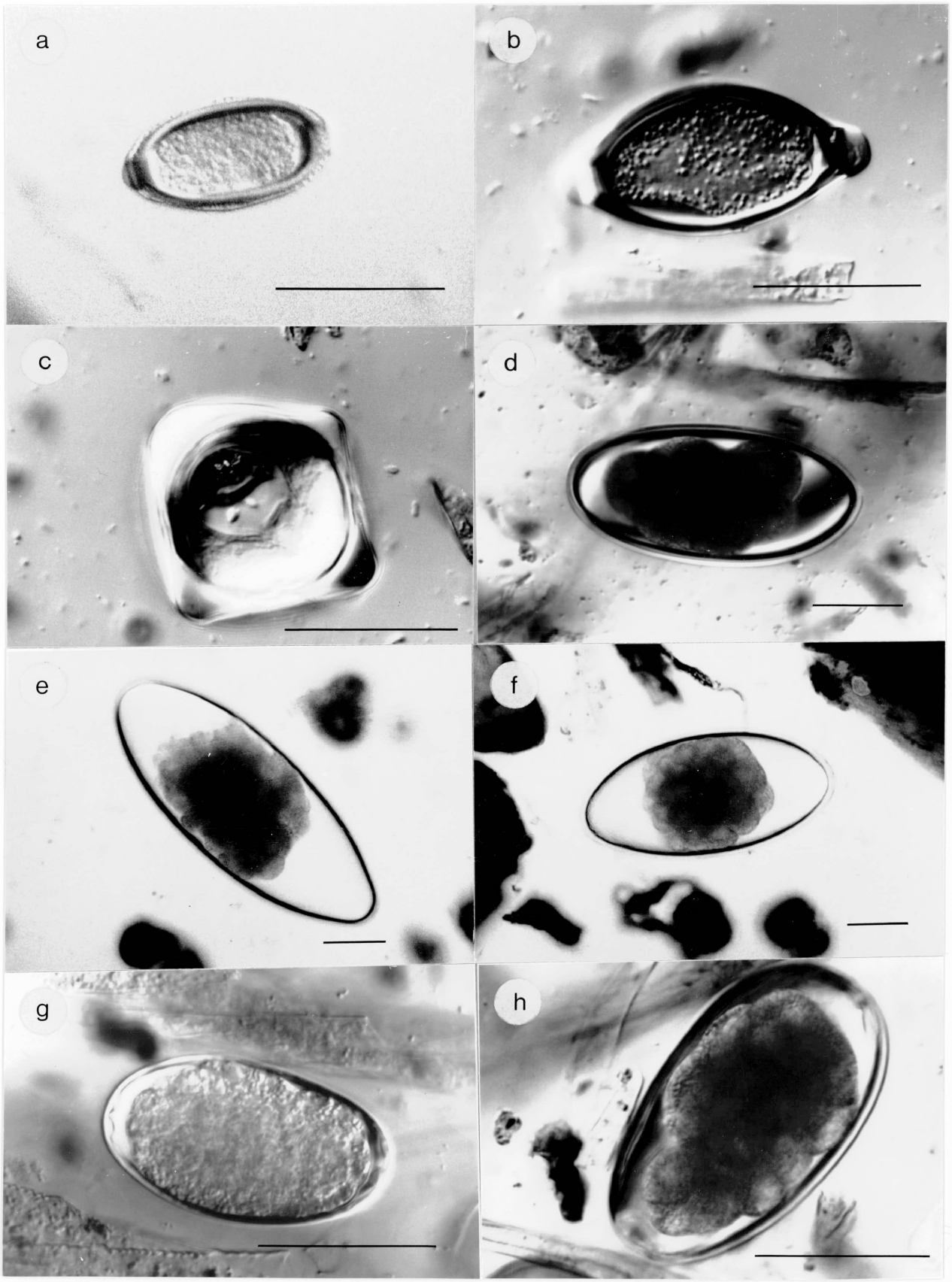

a
b
c
d
e
f
g
h

Table 4. Mean dimensions ($\mu$m) of gastro-intestinal helminth eggs recovered by fecal flotation from wild and captive caribou at different locations.

| Species | Source[a] | length[b] | width |
|---|---|---|---|
| *Nematodirella longissimespiculata* | Slate | 263 (240-301) | 123 (108-149) |
| | NWT | 258 (238-283) | 114 (105-121) |
| | Topsails | 251 (230-272) | 113 (100-120) |
| *Nematodirella alcidis* | Moose | 248 (215-268) | 113 (105-120) |
| *Nematodirus tarandi* | NWT | 207 (186-228) | 100 (92-108) |
| *Nematodirus odocoilei* | Captive | 159 (148-180) | 75 (68-82) |
| | Topsails | 159 (140-179) | 77 (70-80) |
| *Nematodirus helvetianus* | Captive | 200 (180-220) | 95 (85-100) |
| *Ostertagia* sp. | Slate | 92 (78-103) | 47 (43-52) |
| Trichostrongylid[c] | Captive | 83 (72-90) | 45 (39-53) |
| *Capillaria* sp. | Slate | 52 (45-58) | 27 (24-30) |
| | Captive | 50 (43-55) | 26 (23-30) |
| | Topsails | 52 (48-57) | 25 (23-29) |
| *Trichuris* sp. | Captive | 71 (67-74) | 34 (30-36) |
| | Top Sails | 72 (70-75) | 34 (32-35) |
| *Monezia* sp. | Slate | 71 (59-98) | 66 (56-85) |
| | NWT | 64 (59-75) | 60 (51-70) |
| | Captive | 64 (50-75) | 61 (43-73) |
| | Moose | 63 (57-70) | 57 (48-64) |
| *Oe. venulosum* | Captive | 100 (90-110) | 56 (45-69) |

[a] All measurements are from caribou unless otherwise stated. Source includes Slate Islands, the Beverly herd, Northwest Territories (NWT) Topsails herd, Newfoundland and captive animals at the Kakabeka Falls Game Farm.

[b] Measurements reported for length and width are the mean of 50 eggs followed by range in parentheses.

[c] May include *Ostertagia* spp., *Trichostrongylus* spp. and *Spiculopteragia* spp.

Infective larvae ($L_3$) were distinguished by their length, the shape of the $L_3$ tail, and the length of the tail sheath (extension of the $L_2$ cuticle beyond the tip of the $L_3$ tail). Larvae of the Nematodirinae were distinguished from those of the Ostertagiinae by the presence of an exceptionally long tail sheath in the former. The two genera of Nematodirinae were distinguished by the mean length of the $L_3$; *Nematodirella* are longer than 900 $\mu$m, and *Nematodirus* are shorter than 850 $\mu$m (Table 5). Although the shape of the tail is similar (Fig. 10b,c), *Nematodirella alcidis* $L_3$ are longer and have a longer tail sheath than those of *N. longissimespiculata* (Table 5). Larvae of *N. tarandi* and *N. odocoilei* and have similar $L_3$ tails, both being cleft deeply compared with that of the other species (Fig. 10a,e). *Nematodirus helvetianus* $L_3$ are distinguished by the shape of the $L_3$ tail (Fig. 10f) but are similar in body length to *N. tarandi.* The position of the anus and the length of the $L_2$ sheath are also diagnostic of *N. helvetianus.* *Ostertagia gruhneri* larvae possess a short tail sheath (27-45 $\mu$m) with a distinctive kink, typical of the genus (Fig. 10d) and range in total length from 923 to 1118 $\mu$m, (Table 5). Infective larvae of *Ostertagia gruhneri* were significantly longer than those of *Ostertagia* spp. cultured from the feces of captive caribou.

*Recovery of adult helminths and seasonal changes in the number of eggs passed in feces*

*Woodland caribou on the Slate Islands*

Seasonal changes in the number of abomasal nematodes present in Slate Islands caribou were observed. Complete abomasa and small intestines from six caribou were available for parasitological examination as well as representative

Table 5. Mean dimensions of infective Trichostrongyloid larvae cultured from the feces of caribou and moose.

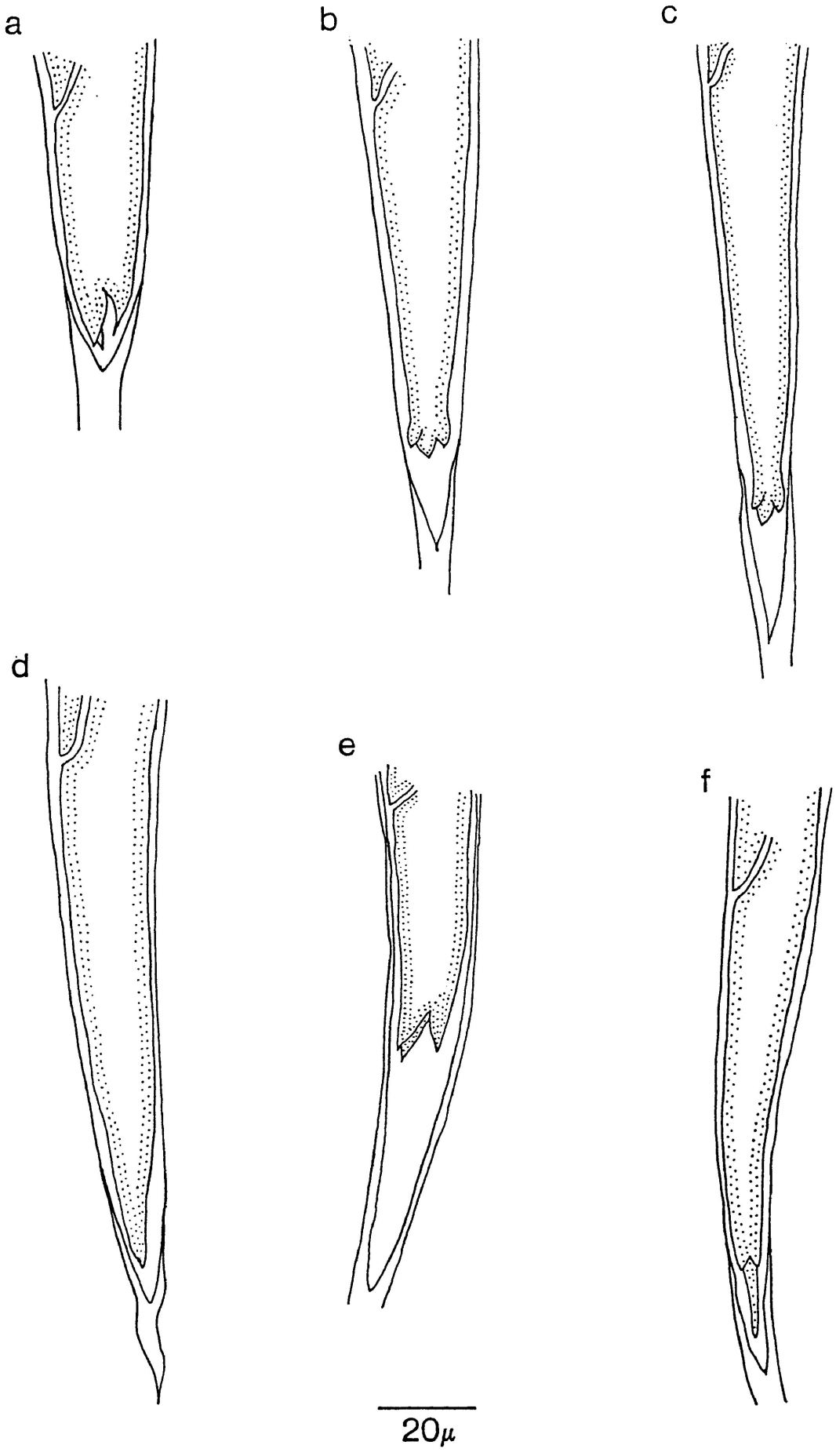
| Species | n | l[a] | ts | nr | ep | es | gp | an |
|---|---|---|---|---|---|---|---|---|
| *Ostertagia gruhneri*[b] | 30 | 1010±11.0 (923-1118) | 36±0.7 (27-40) | 132±1.6 (110-145) | 148±3.5 (130-160) | 205±1.8 (175-225) | 567±9.9 (470-660) | 87±1.8 (70-100) |
| *Ostertagia leptospicularis*[c] | 24 | 776±11.1 (680-900) | 51±2.2 (35-80) | 111±2.0 (100-120) | 122±2.0 (110-135) | 176±1.9 (160-200) | 426±7.9 (370-465) | 78±1.5 (65-95) |
| *Nematodirella longissimespiculata* | 30 | 980±9.7 (850-1075) | 346±6.9 (275-430) | 161±1.7 (150-175) | 180±2.1 (160-195) | 251±3.0 (225-280) | 573±6.3 (520-630) | 76±0.9 (68-80) |
| *Nematodirella alcidis* | 30 | 1147±8.3 (1065-1220) | 497±8.2 (445-655) | 154±1.7 (140-170) | 182±1.6 (165-200) | 239±2.2 (220-265) | 617±5.9 (555-650) | 98±1.6 (85-120) |
| *Nematodirus tarandi* | 16 | 821±7.8 (750-870) | 355±10.0 (275-415) | 149±2.2 (135-160) | 168±2.8 (150-195) | 231±2.4 (210-250) | 494±5.2 (450-520) | 51±0.3 (49-52) |
| *Nematodirus odocoilei* | 24 | 731±5.5 (660-790) | 295±14.2 (180-390) | 132±4.6 (125-150) | 152±7.3 (140-180) | 211±2.4 (205-215) | 452±10.2 (430-490) | 55±1.8 (50-60) |
| *Nematodirus helvetianus* | 14 | 819±7.4 (755-860) | 222±6.8 (200-250) | 128±3.3 (110-140) | 143±3.8 (125-160) | 214±6.2 (185-230) | 473±9.2 (435-500) | 79±2.9 (60-90) |

[a] All measurements are in µm (mean±standard error subtended by range). Abbreviations include l, length of $L_3$; ts, extension of tail sheath beyond $L_3$ tail; nr, nerve ring; ep, excretory pore; es, esophagus; gp, genital primordia; an, distance from anus to tip of $L_3$ tail.

[b] May include up to 3% *Ostertagia arctica*.

[c] May also include *Ostertagia kolchida, O. gruhneri, O. arctica, Spiculopteragia* spp. and *Trichostrongylus* spp..

Fig. 10. Caudal end (left lateral view) of infective larvae of Trichostrongyloidea parasitizing caribou and moose. (a) *Nematodirus tarandi*; (b) *Nematodirella longissimespiculata*; (c) *Nematodirella alcidis*; (d) Ostertagia gruhneri/arctica; (e) *Nematodirus odocoilei*; (f) *Nematodirus helvetianus*.


a
b
c
d
e
f
20μ

collections of nematodes from five animals that died between 1977 and 1980. Animals examined had from 960 to 7440 (3247±935) adult *Ostertagia* spp. (Table 6). Adult *Ostertagia* were most numerous during the fall and declined over winter. *Ostertagia gruhneri* was recovered in all animals and comprised 97-100% of the total number of mature worms. *Ostertagia arctica* was detected in 7/11 animals and never comprised more than 3% (4-73 worms) of the total number of male worms counted. Sex ratios of *Ostertagia* spp. ranged from 26-49% (37±3.6) males.

Inhibited fourth-stage larvae of *Ostertagia* spp. were recovered from the abomasa of five animals examined (Table 6). Numbers ranged from 590 to 9270 (4715±2358) and comprised from 9-85% of the total abomasal nematode population (adults and $L_4$). The highest and lowest number of inhibited larvae were recovered in the winter and spring respectively (Table 6). The mean length of inhibited larvae was 1.35 mm (1.14-1.63).

Fecal examination revealed that the intensity of infection (EPG) and prevalence of helminth ova also varied with season. A total of 353 fecal samples were examined from 1984 to 1986 (Appendix 1). Eggs of *Ostertagia* spp. were detected in the feces of all adult caribou examined from May to October (Fig. 11). No helminth ova were detected in two calves sampled 25 June, 1986 when they were 2-5 weeks old. The lowest prevalence of *Ostertagia* spp. was observed during late winter (March and April) (Fig. 11). Monthly mean fecal egg counts varied seasonally and were significantly higher in spring, summer and fall than in late winter (Fig. 12). Mean egg counts were similar for samples taken from April to August. A distinct peak occurred during September, 1985 (Fig. 12). The largest number of *Ostertagia* eggs observed was 1399 EPG in the feces of a calf during July 1985.

Table 6. Number of gastro-intestinal nematodes and fecal egg counts (EPG) from wild caribou examined from the Slate Islands.

| | | | *Ostertagia* spp.[a] | | | *Nematodirella longissimespiculata* | |
|---|---|---|---|---|---|---|---|
| Date | Age | Sex | Adult | $L_4$[b] | EPG | Adult | EPG[c] |
| Sep/85 | 2.5 | M | 7440 | 700 | 1270 | 870 | 330 |
| Sep/85 | 7.5 | F | 3020 | 8300 | 590 | 0 | 0 |
| May/85 | 2.0 | F | 2650 | 590 | 68 | 0 | 0 |
| Feb/85 | 0.5 | M | 960 | P[d] | 5 | P | 165 |
| Feb/85 | 2.5 | M | 1600 | 9270 | 0 | 1220 | 75 |
| Nov/84 | Adult | M | 3810 | 0 | 0 | -[e] | |
| Sep/80 | Adult | M | P | | | 0 | 0 |
| Oct/79 | Adult | F | P | | | P | |
| Oct/79 | 0.5 | M | P | | | P | |
| Oct/79 | 0.5 | F | P | | | P | |
| Oct/77 | 3.5 | F | P | | | 0 | |

[a] Includes *Ostertagia gruhneri* and *Ostertagia arctica.*

[b] Estimated number of inhibited fourth-stage larvae ($L_4$) free in the lumen of the abomasum based on ratio of $L_4$: adults in small unscreened subsamples.

[c] Eggs/g of dry feces.

[d] P indicates that species was present but not counted.

[e] Material not available for examination.

Fig. 11. Seasonal changes in the prevalence of gastro-intestinal helminth ova in the feces of Slate Island caribou.

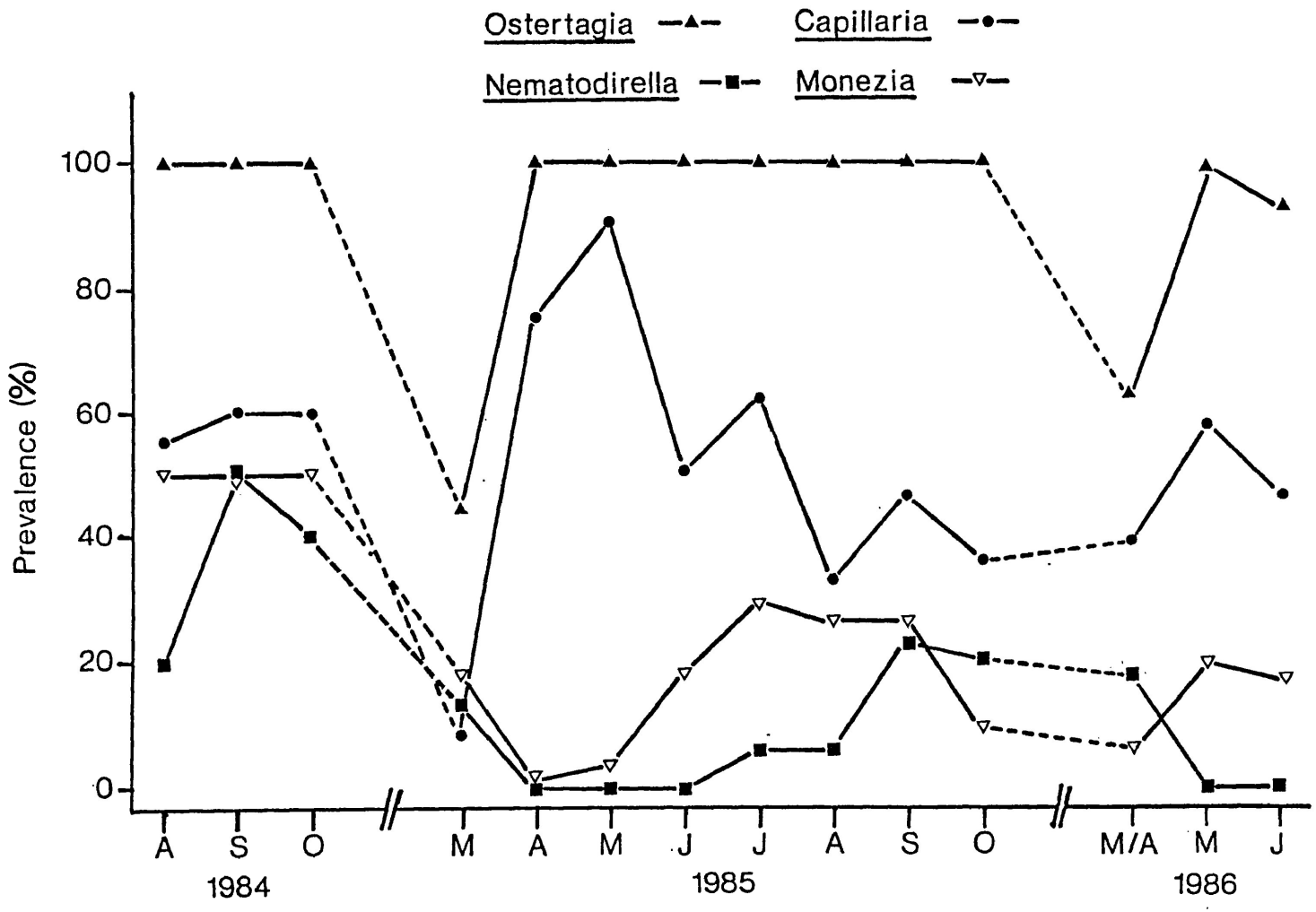
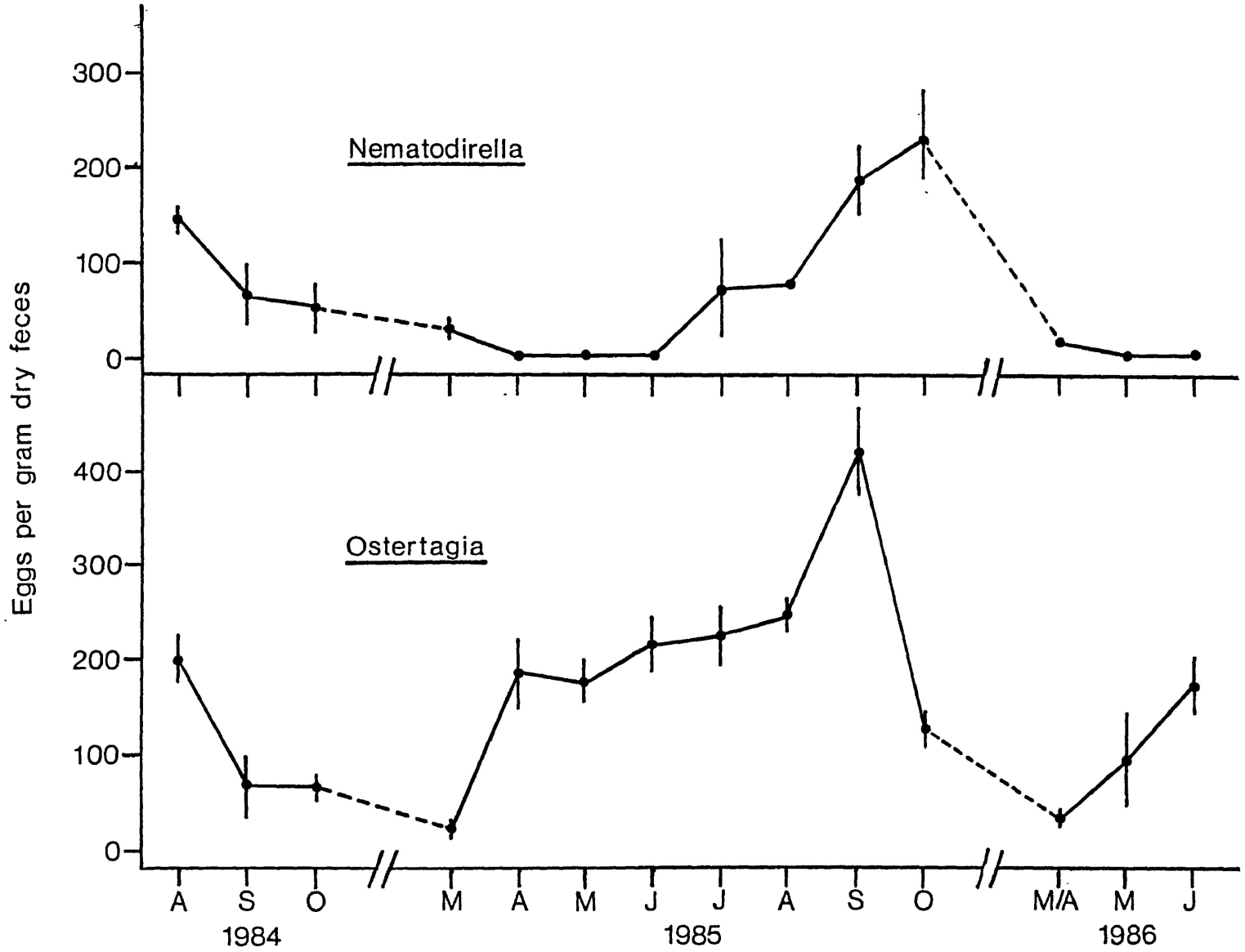

Ostertagia
Capillaria
Nematodirella
Monezia
Prevalence (%)
100
80
60
40
20
0
A
S
O
M
A
M
J
J
A
S
O
M/A
M
J
1984
1985
1986

Fig. 12. Seasonal changes in the monthly mean number of nematode ova (EPG) passed in the feces of Slate Islands caribou. Vertical bars represent $\pm$ 1 standard error.


Eggs per gram dry feces
300
200
100
0
Nematodirella
400
300
200
100
0
Ostertagia
A
S
O
M
A
M
J
J
A
S
O
M/A
M
J
1984
1985
1986

Feces of calves and adults were distinguished by dry pellet weights recorded from both captive and wild animals. Dry pellet weights collected from July to October from known calves ranged from 0.03-0.175 g (0.08±0.005, n=51) (Appendix 2). Dry pellet weights from known adult wild caribou ranged from 0.16-0.335 g (0.23±0.015, n=10). To avoid overestimating the number of calf samples collected, all pellets weighing < 0.14 g were assumed to be from calves.

Combined fecal egg counts of *Ostertagia* spp. from July to October 1985 were significantly higher in calves than in adults ($F_{1,143}$=26.1) (Table 7). Combined fecal egg counts of *Nematodirella* were not significantly different between calves and adults ($F_{1,15}$=4.41).

*Nematodirella longissimespiculata* was found in all calves examined and in three of seven adults whose small intestines were available for examination (Table 6). Counts of *N. longissimespiculata* were not available from calves. However, two adult males collected in fall and early winter each harboured more than 800 worms (Table 6).

The prevalence and intensity of *Nematodirella* ova in caribou feces was highest in the fall and lowest during the spring. Eggs of *Nematodirella* were not detected during April, May or June (Figs. 11,12), but were detected in 15.7% (n=217) of feces examined from July to October, 1975-1985. Of these, 96% of calves and 5.2% of adults were infected (Table 8). The prevalence of *Nematodirella* was significantly higher in calves ($X^2_1$=107.4) and lower in adults ($X^2_1$=14.0) than would be expected by chance. Prevalence in males was significantly higher ($X^2_1$=10.0) than for all adults combined. Prevalence in females was not different from that expected in adults ($X^2_1$=0.2).

Table 7. Comparison of fecal egg counts (eggs/g of dry feces) from calf and adult caribou of the Slate Islands, 1985.

| | Calf | | | Adult | | |
|---|---|---|---|---|---|---|
| Month | n | *Ostertagia* | *Nematodirella*[a] | n | *Ostertagia* | *Nematodirella* |
| Jul. | 1 | 1399[b] (-) | 182 (-) | 52 | 198 (20-974) | 36 (23-49) |
| Aug. | 2 | 397 (217-576) | 126 (-) | 32 | 207 (67-447) | 58 (-) |
| Sep. | 5 | 763 (474-1078) | 194 (121-274) | 30 | 358 (51-1272) | 158 (16-330) |
| Oct. | 4 | 168 (78-260) | 228 (145-368) | 19 | 113 (9-478) | 0 (-) |

[a] Prevalence of *Nematodirella* is given in Table 8.

[b] Mean subtended by range

Table 8. Prevalance (%) of *Nematodirella longissimespiculata* ova in the feces of calf and adult caribou of the Slate Islands.

| | | | Adult | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Calf | | Male | | Female | | Unknown[a] | |
| Date | n | % | n | % | n | % | n | % |
| Oct. /75 | 2 | 100 | 5 | 0 | 4 | 0 | 1 | 0 |
| Jul. /78 | 1 | 100 | 0 | -[b] | 5 | 0 | 4 | 0 |
| Sep. /78 | 5 | 100 | 8 | 13 | 7 | 14 | 6 | 0 |
| Sep. /80 | 0 | | 3 | 33 | 0 | | 9 | 0 |
| Oct. /80 | 5 | 100 | 2 | 50 | 6 | 0 | 0 | |
| Jul. /85 | 1 | 100 | 0 | | 0 | | 52 | 4 |
| Aug. /85 | 2 | 50 | 0 | | 0 | | 32 | 3 |
| Sep. /85 | 5 | 100 | 2 | 100 | 10 | 0 | 17 | 6 |
| Oct. /85 | 4 | 100 | 0 | | 2 | 0 | 17 | 0 |
| Total | 25 | 96 | 20 | 25 | 34 | 3 | 138 | 3 |

[a] Includes amorphous feces and pellets classified as adult but not to sex.

[b] No samples available.

Adult specimens of *Monezia* sp. and *Capillaria* sp. were not recovered although ova of these helminths were present in feces (Table 1, Fig. 11). The prevalence of *Monezia* sp. varied with season and was generally lowest during early spring (Fig. 11). The prevalence of *Capillaria* sp. was generally highest during early spring and lowest during winter (Fig. 11). *Monezia* and *Capillaria* ova were each found in 8% of calf fecal samples examined from July to October, 1985 (n=12) but were present in 26% and 48%, respectively, of adults examined during the same period (n=133). Ova of *Trichuris* sp. were not commonly encountered (2 of 353 samples).

Concurrent infections with *Nematodirella, Capillaria* and *Monezia* were not observed. Of 17 samples with *Nematodirella* collected from July to October 1985, six had *Capillaria* and one had *Monezia.* Concurrent infections of *Monezia* and *Capillaria* were found in 18 of 145 samples collected during this period.

Adult *Dictyocaulus viviparus* were recovered in low numbers (5-30) from 3 of 3 calves and 1 of 6 adults whose lungs were available for examination. Worms recovered during the winter months were shorter ($17.3 \pm 1.3$ mm) than those recovered during the fall ($54.1 \pm 1.6$ mm), and were probably in a state of arrested development. No pathological changes associated with infection were noted.

*Other woodland caribou herds*

The prevalence of *Ostertagia* in other herds of woodland caribou examined showed seasonal fluctuations similar to those seen on the Slate Islands (Table 9). Trichostrongylid eggs were not detected in samples collected during December and February, but were found in 3 of 16 samples from March and

Table 9. Prevalence (%) and intensity (EPG) and of gastro-intestinal helminth ova in feces of woodland caribou herds examined from Northwestern Ontario.

| Location | Date | n | *Ostertagia* spp. | | *Nematodirella* sp.[b] | | *Capillaria* sp. | *Monezia* sp. |
|---|---|---|---|---|---|---|---|---|
| | | | % | EPG[b] | % | EPG | % | % |
| Pukaskwa | May/85 | 13 | 77 | 187 | 0 | 0 | 0 | 0 |
| | Jun/85 | 6 | 100 | 130 | 0 | 0 | 0 | 50 |
| | Oct/84 | 15 | 93 | 24 | 0 | 0 | 0 | 50 |
| | Dec/83 | 3 | 0 | 0 | 33 | 64 | 0 | 33 |
| Pic Is. | Feb/86 | 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Apr/85 | 10 | 100 | 184 | 0 | 0 | 0 | 0 |
| | May/85 | 13 | 100 | P[c] | 0 | 0 | 0 | 0 |
| Schreiber | Jun/85 | 3 | 100 | 149 | 0 | 0 | 100 | 100 |
| Armstrong | Mar/85 | 14 | 14 | 5 | 14 | 52 | 7 | 29 |
| Red Lake | Mar/86 | 2 | 50 | P | 0 | 0 | 0 | 0 |
| Total | | 89 | 66 | | 3 | | 4 | 21 |

[a] Likely all *N. longissimespiculata.*

[b] Eggs/g of dry feces.

[c] P indicates that eggs were present but samples were frozen and fecal egg count is not applicable.

77-100% of samples collected from April to June (Table 9). *Nematodirella* was not as prevalent in these herds as it was on the Slate Islands. *Monezia* and *Capillaria* were found in 21% and 4% of samples respectively. *Trichuris* sp. was detected in only 1 of 15 samples collected from the Pukaskwa herd during October 1984.

Samples collected during January, 1986 (n=30) from woodland caribou of the Topsails herd, Newfoundland, contained ova of *Nematodirus odocoilei* (20%), *Nematodirella longissimespiculata* (7%), *Capillaria* sp. (40%), *Trichuris* sp. (10%) and *Monezia* sp. (3%). Trichostrongylid ova were only detected in 1 of 30 samples. Concurrent infections of *Nematodirus*, *Nematodirella*, *Capillaria* and *Trichuris* were common. Mean egg counts of *N. odocoilei* and *N. longissimespiculata* were 36 and 51 EPG respectively.

*Barren-ground caribou*

Low numbers of abomasal nematodes were recovered from all adult caribou (n=9) examined from the Beverly herd; none was recovered in a calf (Table 10). Inhibited larvae were not recovered. *Ostertagia gruhneri* predominated in all infected animals while *Ostertagia arctica* occurred in 4 of 9 animals and never comprised more than 10% (16 to 32 worms) of the total number of male *Ostertagia* spp. (Table 10). *Teladorsagia circumcincta* was found in 67% of adult animals. Only the calf was infected with *Nematodirella longissimespiculata* and *Nematodirus tarandi* (Table 10).

Three types of helminth ova were detected in the feces of Beverly caribou. Eggs of *N. longissimespiculata* and *N. tarandi* were recovered from 46% and 85% of calves respectively (Table 11). Nematodirinae infected 11% of yearlings and were not detected in animals older than 2.5 years. Patent

Table 10. Estimated numbers of worms recovered at necropsy from barren-ground caribou of the Beverly herd examined during March, 1985.

| Sex | Age | Ostertagia spp.[a] | | | *Teladorsagia circumcincta* | Nematodirinae |
|---|---|---|---|---|---|---|
| | | O.g. | O.a. | F | | |
| F | <1 | 0 | 0 | 0 | 0 | 260[b] |
| F | 2+ | 272 | 29 | 258 | 0 | 0 |
| M | 3+ | 14 | 0 | 55 | 21 | 0 |
| F | 4+ | 141 | 16 | 125 | 31 | 0 |
| F | 4+ | P[c] | P | P | P | 0 |
| F | 4+ | 150 | 0 | 15 | 60 | 0 |
| M | 4+ | 105 | 0 | 182 | 0 | 0 |
| F | Adult | 30 | 0 | 45 | 45 | 0 |
| F | Adult | 486 | 0 | 468 | 35 | 0 |
| M | Adult | 291 | 32 | 420 | 0 | 0 |
| Mean±S.E. | | 186±55 | 26±5 | 184±64 | 38±7 | |

[a] *Ostertagia* includes male *Ostertagia gruhneri* (O.g.), male *Osteragia arctica* (O.a), and female *Ostertagia* spp. (F).

[b] These included 124 male *Nematodirus tarandi*, 4 male *Nematodirella longissimespiculata*, 126 unidentified female Nematodirinae and 6-fourth-stage larvae.

[c] No estimate available.

Table 11. Prevalence (%) and mean intensity (EPG) of *Nematodirus tarandi*, *Nematodirella longissimespiculata* and *Monezia* sp. in barren-ground caribou of the Beverly herd as determined by eggs in feces.

| | | | *Nematodirus* | | *Nematodirella* | | *Monezia* |
|---|---|---|---|---|---|---|---|
| Month | Age | n | % | EPG[a] | % | EPG | % |
| December (1984-1986) | <1 | 5 | 100 | 41 | 20 | 52 | 60 |
| | 1+ | 16 | 6 | 14 | 0 | 0 | 18 |
| | 2+ | 17 | 6 | 3 | 0 | 0 | 12 |
| | >3 | 61 | 0 | 0 | 0 | 0 | 0 |
| total | | 99 | 7 | 32 | 1 | 0 | 8 |
| March (1985-1986) | <1 | 8 | 75 | 27 | 63 | 28 | 13 |
| | 1+ | 11 | 18 | 15 | 9 | 25 | 0 |
| | 2+ | 14 | 0 | 0 | 0 | 0 | 0 |
| | >3 | 51 | 0 | 0 | 0 | 0 | 0 |
| total | | 84 | 10 | 24 | 7 | 28 | 1 |

[a] Eggs/g of dry feces.

infections of *N. longissimespiculata* were rarely detected during December (Table 11). Concurrent infections of *N. longissimespiculata* and *N. tarandi* were commonly encountered during March. *Monezia* sp. was rare in March collections but infected 60% of calves and 4% of animals 1 year of age or older during December (Table 11). Trichostrongylid ova were not recovered in fecal samples from the Beverly herd. Feces from migratory caribou collected near the Kettle River, Manitoba, contained from 2 to 54 trichostrongylid EPG (29±13).

*Captive caribou*

Seasonal fluctuations in egg counts observed in captive caribou were similar to those in animals on the Slate Islands. Trichostrongylid ova (Ostertagiinae and *Trichostrongylus* spp.) were detected in the feces of all captive adult caribou during all months sampled (Fig. 13). Egg counts from adult caribou were lowest during the winter months, increased during late winter and early spring and peaked during the fall (Fig. 13). During 1984, fall peaks in individual adult caribou occurred from 8 to 29 October and ranged from 180-803 EPG (428±105). Fall peaks during 1985 occurred from 4 September to 23 October and ranged from 260-575 EPG (457±60).

Newborn caribou passed trichostrongylid ova as early as 32 and 35 days of age in 1985 and 1986, respectively. Trichostrongylid ova were most numerous in calf feces during September (5017±209) (Fig. 14). The highest individual fecal egg counts from calves were 7670, 6570 and 6250 EPG (6830±431), all of which occurred on 18 September 1985.

Two types of *Nematodirus* ova were identified in the feces of captive caribou. Eggs of *Nematodirella* spp. were not found in the feces of captive

Fig. 13. Seasonal changes in the monthly mean number of nematode eggs passed in the feces of captive adult caribou.

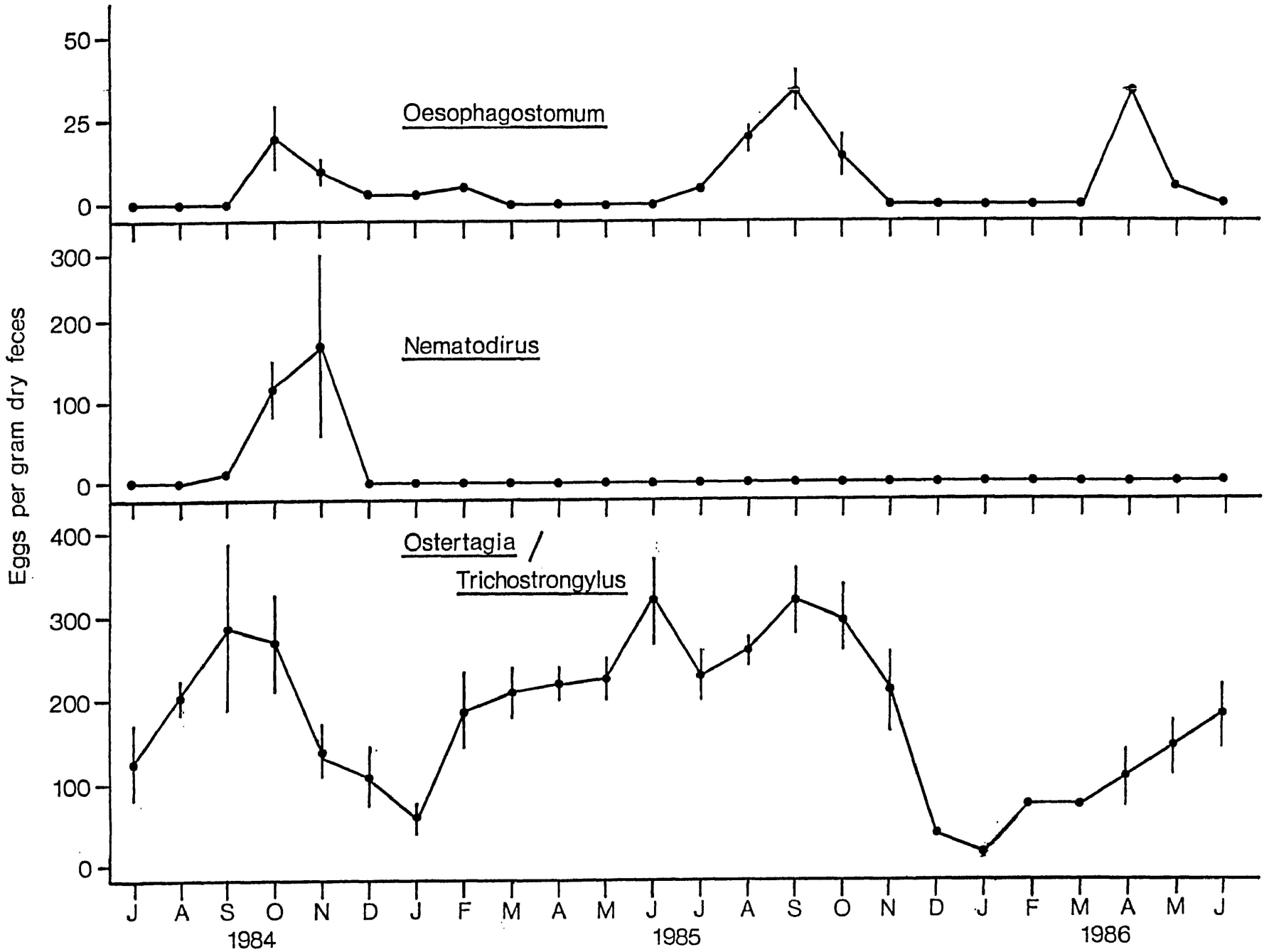
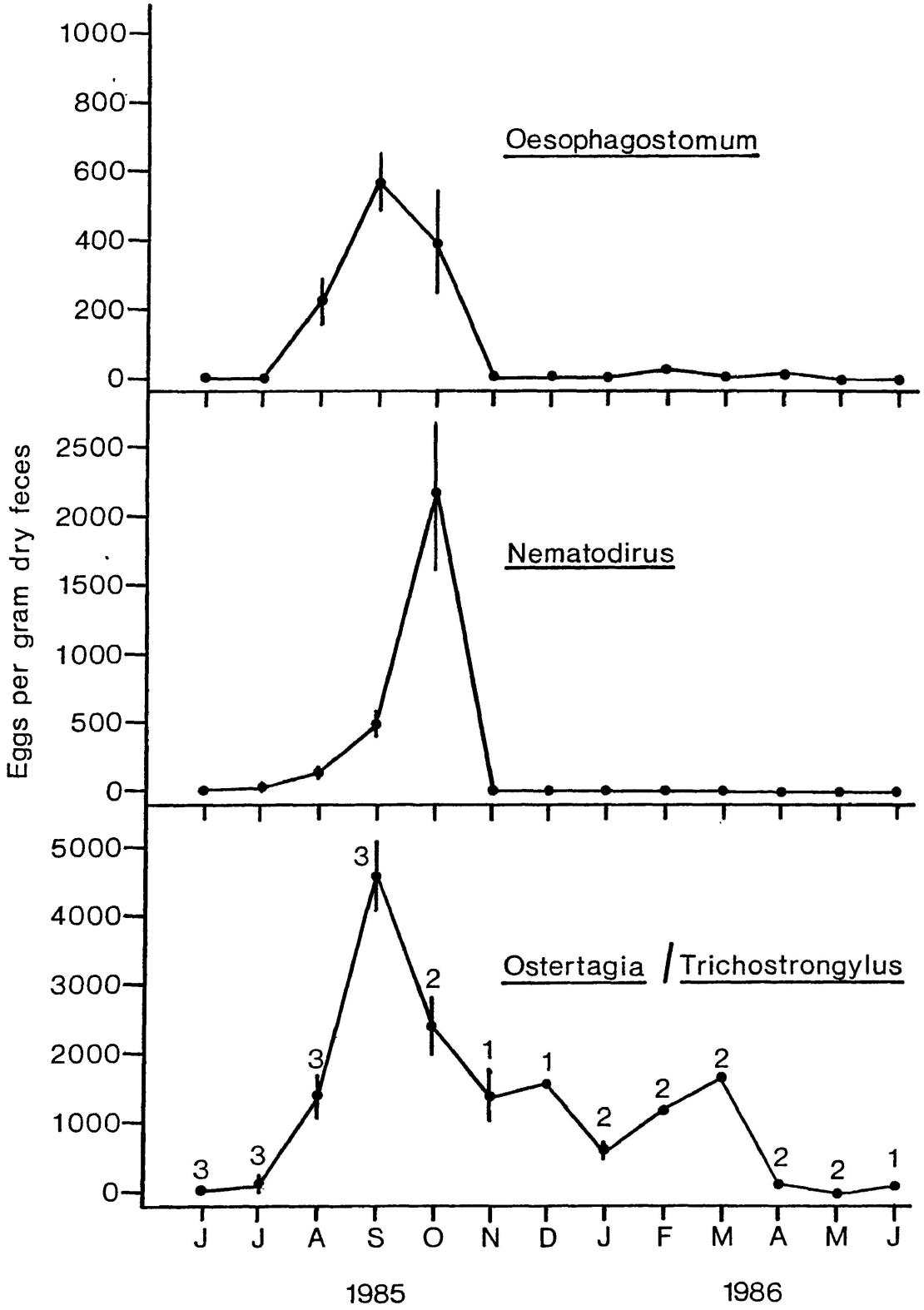

Eggs per gram dry feces
50
25
0
Oesophagostomum
300
200
100
0
Nematodirus
400
300
200
100
0
Ostertagia / Trichostrongylus
J A S O N D J F M A M J J A S O N D J F M A M J
1984
1985
1986

Fig. 14. Seasonal changes in the monthly mean number of nematode eggs passed in the feces of captive caribou calves. (Number of calves available for sampling in each month is indicated above S.E. bars. Both calves were treated with Ivomec April 18, 1986)


Eggs per gram dry feces
1000
800
600
400
200
0
Oesophagostomum
2500
2000
1500
1000
500
0
Nematodirus
5000
4000
3000
2000
1000
0
Ostertagia / Trichostrongylus
3
3
3
2
1
1
2
2
2
2
1
J J A S O N D J F M A M J
1985
1986

caribou except in two wild calves brought into captivity during October of 1985. During the fall of 1984, all caribou acquired infections of *Nematodirus odocoilei.* Infections were relatively short lived in adult caribou (Fig. 13), lasting from one to four weeks. Maximum fecal egg counts of *N. odocoilei* in adult caribou ranged from 6-432 EPG (139±67). During 1984, three captive calves from Newfoundland also developed patent infections of *N. odocoilei.* Although these calves were not monitored on a regular basis, maximum observed egg counts ranged from 85-576 EPG (392±154). Two yearlings, each experimentally infected with 100 infective larvae of *Nematodirella longissimespiculata*, did not develop patent infections.

No adult caribou (> 1 yr old) had a *Nematodirus* infection during 1985 or 1986 (Fig. 13). Calves born during the spring of 1985 acquired mixed infections of *N. odocoilei* and *N. helvetianus* by the end of July. No attempt was made to separate egg counts by species due to the large numbers of eggs encountered (Fig. 14). The maximum number of *Nematodirus* eggs passed by the three calves were 603, 944 and 3625 EPG. Egg numbers declined rapidly after the peak had been reached in the calf which was not treated with Ivomec.

Calves acquired patent infections of *Trichuris* sp., *Capillaria* sp. and *Monezia* sp. during their first summer and fall. *Trichuris* was first detected at 53-80 days of age and lasted 5-8 weeks. No adults passed eggs of *Trichuris. Capillaria* infections were first detected at 88-101 days. *Monezia* sp. infections were first detected in calves from mid-August to mid-September (87-115 days). *Capillaria* sp. and *Monezia* sp. were present in adult animals during all months of the year.

*Oesophagostomum* sp. eggs were detected in calves from the beginning of

August to the end of October (Fig. 14). All calves were infected by 73 to 80 days of age; maximum fecal egg counts ranged from 806-1145 EPG (973±98) in calves (Fig. 14). *Oesophagostomum* sp. was also present in all adults during the same late summer and fall period, but maximum egg counts were only 29 to 91 EPG (48±11) (Fig. 13).

*Mortality of captive caribou*

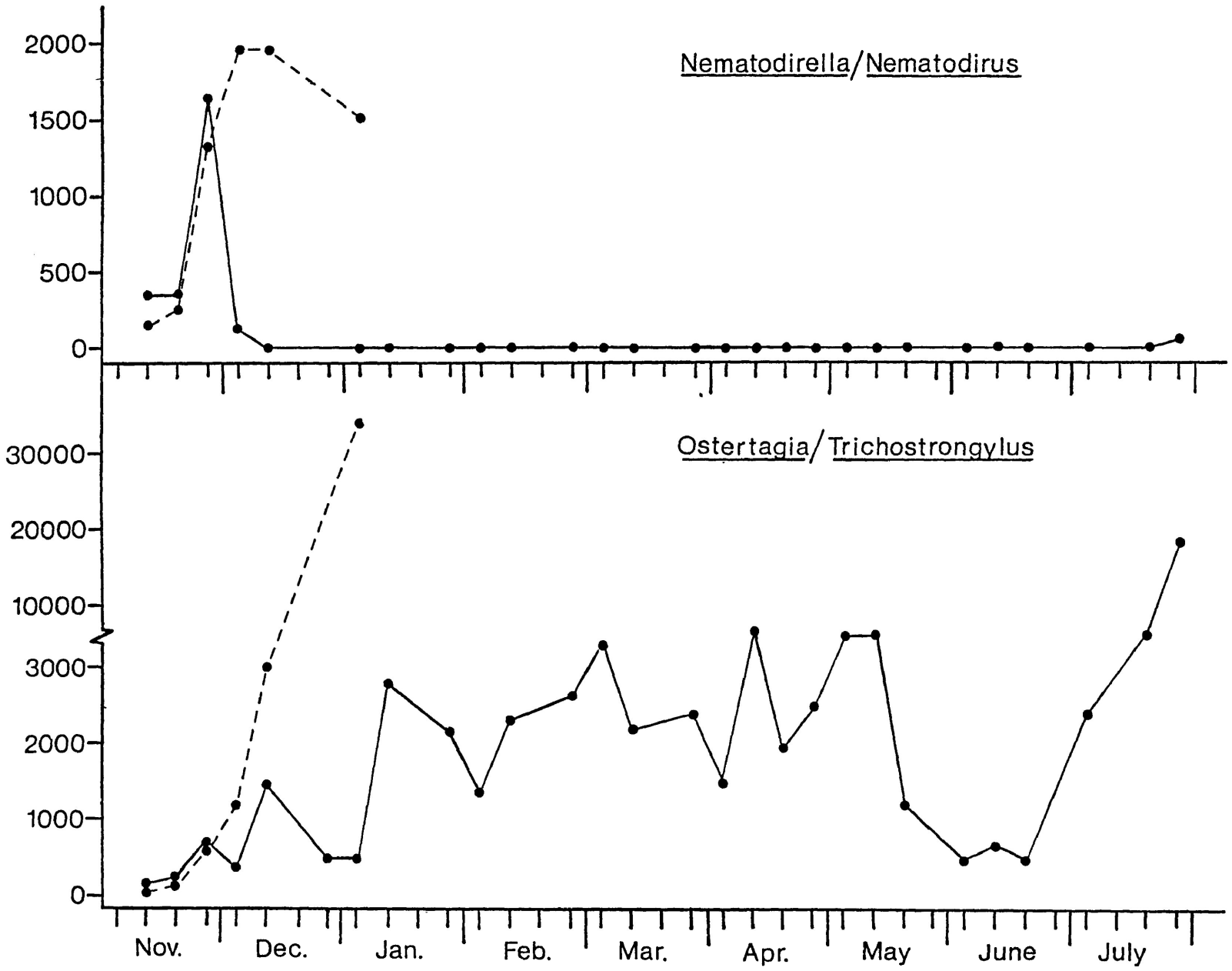
Evidence of disease caused by abomasal nematodes of the genus *Ostertagia* was observed in four captive animals during the course of the study. The history of all animals suggested that stress as well as unusually high numbers of nematodes were important factors in their deaths.

Two wild calves (one male, one female) captured on the Slate Islands were transferred to the Kakabeka Falls Game Farm during October, 1985. They were placed in a pen occupied by caribou earlier that year. During the ensuing three months, the male calf appeared to adapt to captivity but the female remained nervous until her death in January 1986.

At the time of capture, egg counts of *Nematodirella* and *Ostertagia* were similar for both animals (Fig. 15). New infections of *N. odocoilei* and *N. helvetianus* were detected by 25 days post transfer and the female continued to pass eggs of these species until she died in January. No eggs of *Nematodirella* or *Nematodirus* were detected in the feces of the male calf by mid December (Fig. 15). Just prior to his death in late July, the male calf again developed a patent infection of *Nematodirus odocoilei.* Eggs of *Trichuris* sp. were detected by mid January in both animals (86 to 90 days post-transfer).

Two other animals, experimentally infected with *Parelaphostrongylus tenuis*, were terminated in August and September. Both of these and the two

Fig. 15. Changes in the number of nematode eggs passed in the feces up to the time of death of two wild calves brought into captivity. (male——; female ---).


Nematodirella/Nematodirus
2000
1500
1000
500
0
Ostertagia/Trichostrongylus
30000
20000
10000
3000
2000
1000
0
Nov.
Dec.
Jan.
Feb.
Mar.
Apr.
May
June
July

found dead were stressed. Causes of stress included leg injury caused by a dart gun, nervousness, posterior paralysis due to infection with *P. tenuis*, and pneumonia. No detectable fat reserves (femur marrow, back or visceral) were observed in any animal.

Abomasal nematodes were recovered in large numbers from animals dying in captivity (Table 12). The predominant nematode in all animals was *Ostertagia leptospicularis* (Table 12). Three of the four animals that died had lesions characteristic of ostertagiiasis spread over the entire fundic region of the abomasum. Lesions were observed on the pyloric region of one animal. Before death, all animals demonstrated a marked rise in fecal egg counts (Fig. 15). From 1 to 230 *Dictyocaulus viviparus* were recovered from the female calf and two male yearlings.

*Gross pathology and histology of the abomasum in wild and captive caribou*

Elongated ulcerative lesions were observed in the lining of the abomasum of several caribou from the Slate Islands. They were dark red in color (Fig. 16a), and ranged from 1 to 2 mm wide and up to 2 cm long and occurred mostly on the crests of the fundic folds. They were rarely seen in the pyloric region. Ulcers were more common in calves than adults. Due to advanced decomposition of the material examined, histological characterization of the lesions was not possible.

Lesions in captive animals were typical of those caused by *Ostertagia* spp. and consisted of individual to confluent nodular thickenings over the entire fundic region (Fig. 16b). Adult nematodes were occasionally observed protruding from gastric glands located in the centre of some nodules. The thickening of the mucosa in affected areas was due to hyperplasia in the distal

Table 12. Estimated number of adult abomasal nematodes recovered from captive caribou.

| | | | Male Ostertagiinae (%)[a] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Age | Sex | Date | O.g. | O.a. | O.l. | O.k. | O.o. | S.s. | Trich[b] | Total[c] | EPG[d] |
| <1 | F | 01/86 | 10 | 0 | 86 | 1 | 3 | 0 | 16070 | 32840 | 34000 |
| 1+ | M | 07/86 | 4 | 1 | 86 | 8 | 1 | 0 | 11000 | 43000 | 18850 |
| 3+ | M | 08/86 | 0 | 0 | 91 | 9 | 0 | 0 | 950 | 19370 | 2630 |
| 1+ | M | 09/86 | 0 | 0 | 81 | 13 | 2 | 4 | 4184 | 62584 | 4681 |

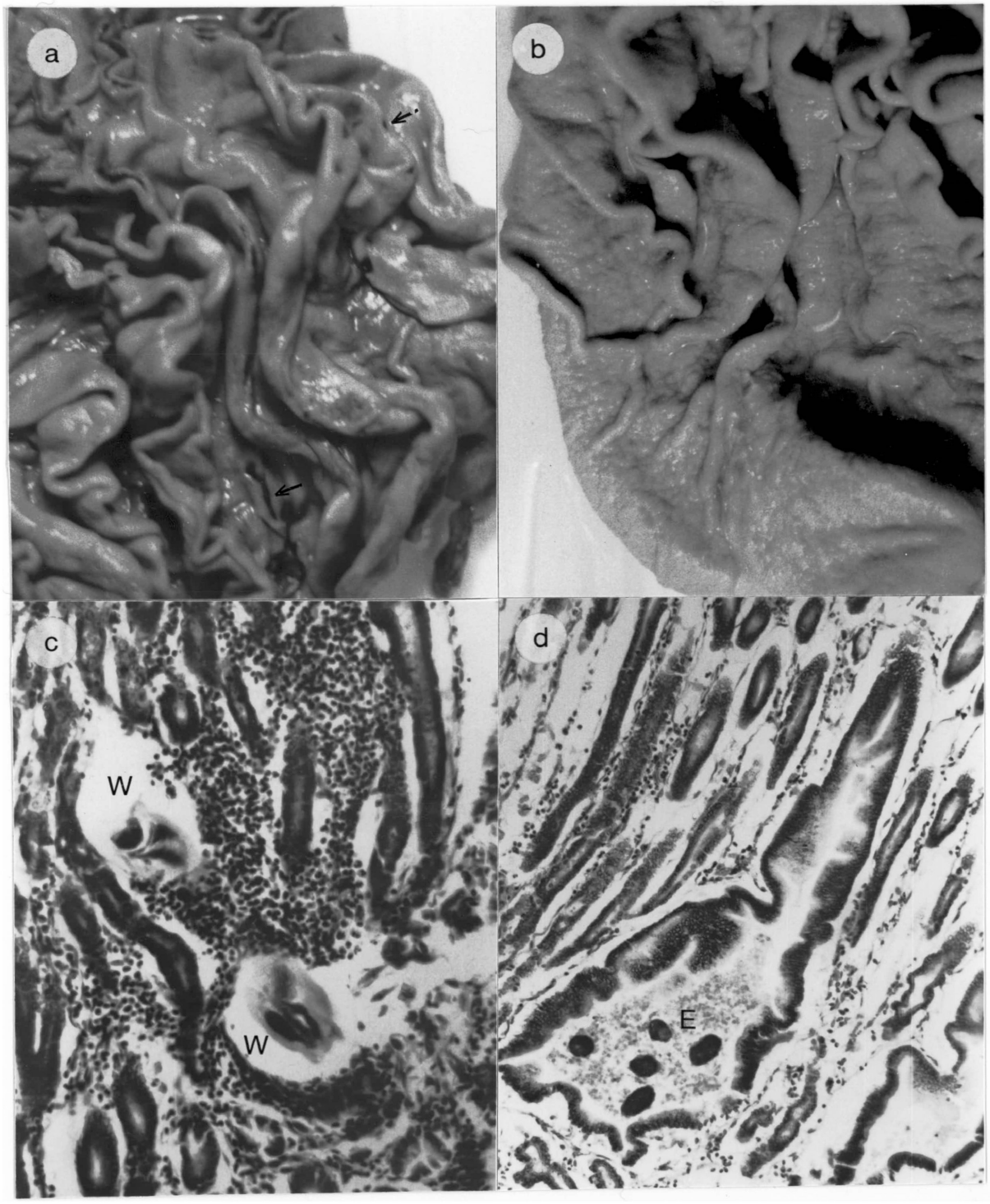
[a] Male Ostertagiinae include *Ostertagia gruhneri*, O.g.; *Ostertagia arctica*, O.a.; *Ostertagia leptospicularis*, O.l.; *Ostertagia kolchida*, O.k.; *Ostertagia ostertagi*, O.o. and *Spiculopteragia spiculoptera*, S.s.

[b] Trich= *Trichostrongylus axei* (males and females).

[c] Estimated total of all adult abomasal nematodes.

[d] Eggs/g of dried feces of abomasal nematodes at time of death.

Fig. 16. Caribou abomasal walls showing lesions (arrows) caused by abomasal nematodes. (a) Wild caribou from Slate Islands. (b) Captive caribou showing morrocan leather like appearance. (c) Section through a parasitized gland showing accumulation of eosinophils around adult *Ostertagia* sp. (W) (captive caribou). (d) Section through parasitized gland showing nematode eggs (E) (captive caribou).


a
b
c
W
W
d
E

end of the gastric glands. Glands in affected areas were devoid of parietal cells. Large accumulations of eosinophils were noted in and between glands. Histological sections revealed adult and larval worms embedded in the mucosa causing distension of the affected glands (Fig. 16c). The presence of adult worms caused the compression of cells lining the affected gland. Adult *Ostertagia* sp. observed embedded in glands were frequently surrounded by large numbers of eosinophils. Distended glands containing nematode eggs surrounded by eosinophils were also observed (Fig. 16d). Numerous aggregations of lymphocytes were observed in the lamina propria.

*Effect of host age, season and herd density on worm morphology*

Both host age and season had a significant effect on the fecundity of female *Ostertagia* spp. (Table 13). Worm length, spicule length and the percentage of females with a vulval flap varied with host age and herd density (Table 13, Fig. 17) but not with season.

During the fall, female worms recovered from caribou calves on the Slate Islands were more fecund than those recovered from adults on the Slate Islands (Table 13, Appendix 3). Worms recovered from an adult animal on Pic Island were intermediate in fecundity between worms from calves and adults on the Slate Islands. There was no significant difference in fecundity of worms recovered from adult caribou on the Slate Islands in the fall and spring (Appendix 3). The fecundity of female worms was lowest during the winter months (November to March) and did not differ between calves and adults from the Slate Islands and adults from the Beverly herd.

In Slate Islands caribou, male and female worms were significantly longer in calves than in adults (Table 13, Fig. 17). Worms from an adult on Pic

Table 13. Effect of host age, locality and season on mean dimensions of female and male *Ostertagia gruhneri* recovered from wild caribou.

| | Female* | | | | Male | |
|---|---|---|---|---|---|---|
| Source | Length (mm)** | Season+ | Fecundity | % Flaps | Length (mm) | Spicule ($\mu$m) |
| Slate | | | | | | |
| Calf (n=3) | 12.31±0.09[a] (90) | F | 44.7±1.86[a] (60) | 66 | 9.11±0.05[a] (80) | 216±0.72[a] (80) |
| | | W | 12.8±1.31[b] (30) | | | |
| Adult (n=8) | 10.11±0.05[b] (224) | S&F | 19.7±0.67[c] (164) | 10 | 8.02±0.04[b] (233) | 192±0.71[b] (233) |
| | | W | 12.1±0.62[b] (60) | | | |
| Pic (n=1) | 11.81±0.12[c] (30) | F | 32.5±1.16[d] (30) | 43 | 8.94±0.07[c] (30) | 214±1.83[a] (30) |
| Beverly (n=9) | 11.83±0.08[c] (114) | W | 13.1±0.59[b] (114) | 77 | 8.91±0.05[c] (101) | 206±2.20[c] (101) |

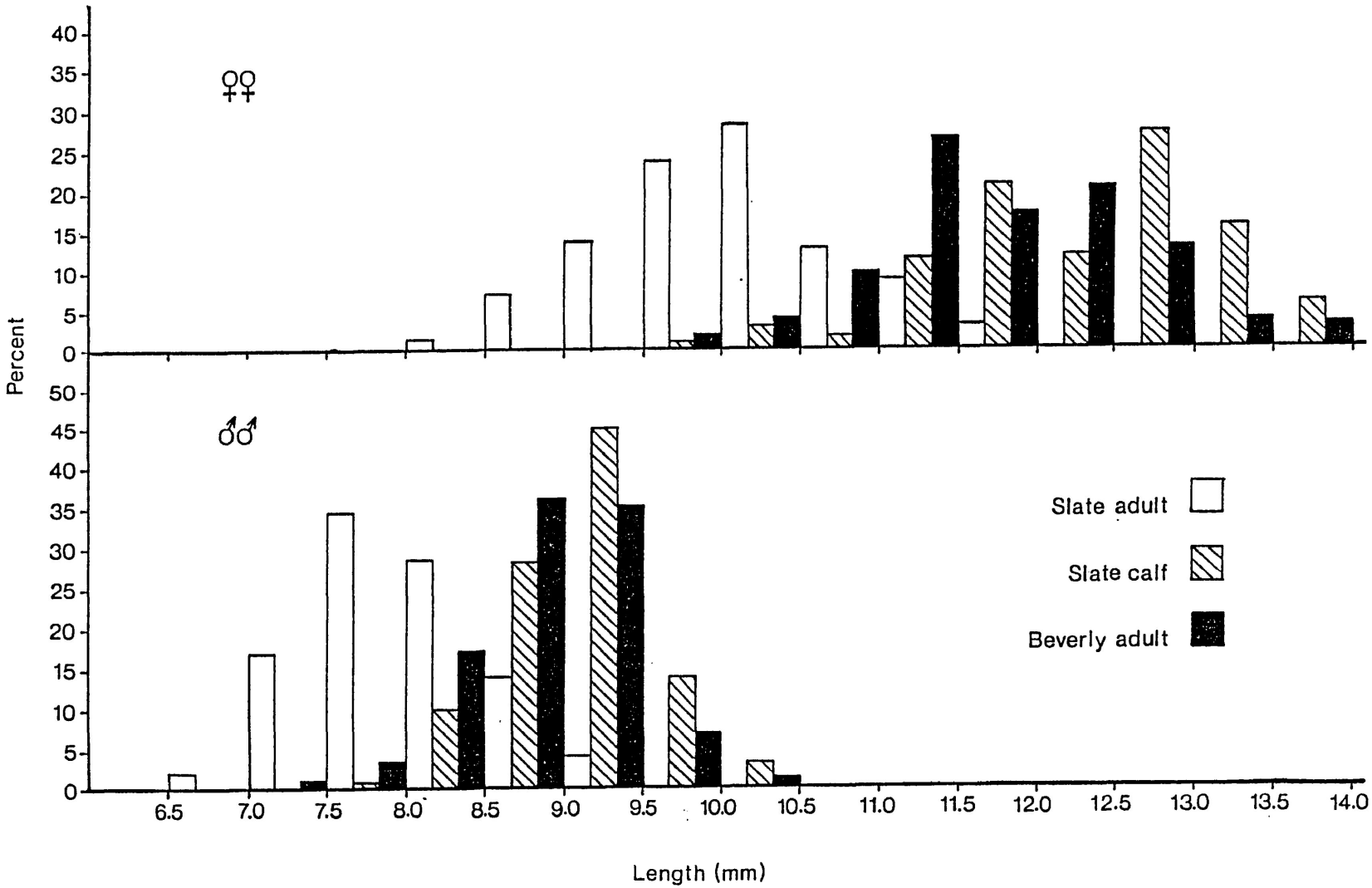
* Females may include up to 3% *Ostertagia arctica* in Slate animals and 5% in Beverly animals.

** Mean±standard error (n).

\+ Seasons include spring (May), fall (August to October) and winter (November to March).

[a] Different superscripts within the same column denote significant differences.

Fig. 17. Frequency distribution (%) of length of male and female *Ostertagia gruhneri* in Slate calf, Slate adult, and adult barren-ground caribou of the Beverly herd.


♀♀
♂♂
Percent
40
35
30
25
20
15
10
5
0
50
45
40
35
30
25
20
15
10
5
0
Slate adult
Slate calf
Beverly adult
6.5
7.0
7.5
8.0
8.5
9.0
9.5
10.0
10.5
11.0
11.5
12.0
12.5
13.0
13.5
14.0
Length (mm)

Island were similar in length to those recovered from barren-ground caribou, but significantly longer than those from adults on the Slate Islands (Table 13). Trends in spicule length were similar to those seen for worm length (Table 13).

Vulval flaps were more common on worms recovered from caribou calves on the Slate Islands (66%) and adult barren-ground caribou (86%) than they were from adult animals on the Slate Islands (8%). Forty-six percent of female worms from Pic Island possessed vulval flaps. A high proportion (>90%) of female *Ostertagia* spp. recovered from captive animals had vulval flaps.

*Biology of the free living stages of trichostrongyles parasitizing caribou and moose*

All species examined demonstrated some degree of resistance to the effects of freezing, dessication or both. Generally *Nematodirella* spp. were more resistant to freezing and dessication as eggs and larvae than *Ostertagia* spp..

Ninety percent of *N. longissimespiculata* third-stage larvae ($L_3$) withstood 30 days of dessication at room temperature (Table 14). Thirty-eight percent of $L_3$'s frozen for 30 days at -18°C survived. All larvae dessicated before freezing survived for 30 days.

Infective larvae hatched from 85% of fresh *N. longissimespiculata* eggs and 26% of eggs frozen for 11 months when incubated at 25°C. Little or no development past the 8-cell stage occurred after incubation for 30 days at 3°C. Eggs cultured at 22, 25, 30 and 35°C first hatched after 17.3, 12.5, 11.0 and 6.5 days of incubation respectively. Less than 10% of eggs incubated for up to 60 days at 25°C in moistened feces demonstrated any degree of development past the $L_1$ stage. Undeveloped eggs subsequently removed from the feces and

Table 14. Survival (%) of the infective larvae of *Ostertagia* sp., *Nematodirella longissimespiculata* and *Nematodirella alcidis* after dessication (D), freezing (F) and freezing with prior dessication (D&F).

| | *Ostertagia* | | | *Nematodirella longissimespiculata* | | | *Nematodirella alcidis* | | |
|---|---|---|---|---|---|---|---|---|---|
| Days | F* | D | D&F | F | D | D&F | F | D | D&F |
| 1 | 100 | 100 | 90 | 90 | 100 | 100 | 100 | 100 | 70 |
| 3 | 80 | 100 | 100 | 90 | 100 | 90 | 100 | 100 | 100 |
| 5 | 90 | 90 | 100 | 80 | 100 | 100 | 10 | 80 | 100 |
| 10 | 80 | 100 | 80 | 70 | 100 | 100 | 20 | 100 | 80 |
| 20 | 40 | 100 | 60 | 67 | 100 | 100 | 10 | 50 | 0 |
| 30 | 0 | 80 | 10 | 38 | 90 | 100 | 0 | 0 | 70 |

* F = frozen at -18°C, D = dessicated at room humidity and temperature.

incubated in distilled water at 25°C were capable of development to the infective stage. First-stage larvae frozen for 7 days within the egg resumed development to the infective stage when returned to 25°C.

Third-stage *Ostertagia* spp. larvae cultured from the feces of wild caribou withstood 30 days of dessication with only 20% mortality (Table 14). No mortality was observed after one day at -18°C. By day 10, 80% were alive but none survived for 30 days. Dessication prior to freezing only slightly enhanced survival with 10% alive after 30 days (Table 14). Chilling prior to freezing produced a 25% increase in survival over controls after 20 days.

Eggs of *Ostertagia* were not capable of withstanding freezing at -18°C. No eggs hatched after one day of freezing. Up to 80% of eggs could not be recovered by flotation after 30 days of freezing.

Poor results were obtained in trials with third-stage *Nematodirella alcidis.* Survival of dessicated larvae declined to 0% by 30 days. Few larvae survived more than 10 days at -18°C (Table 14). Dessication prior to freezing appeared to enhance larval survival.

Eggs of *N. alcidis* were capable of hatching as infective larvae after 600 days of freezing. Due to the small number of eggs generally encountered in moose feces, further experiments were not conducted.

An attempt was made to culture eggs of *Nematodirus tarandi*, collected from the Northwest Territories. Eggs frozen for at least 90 days developed to the infective stage. Few eggs of this species were available which did not permit further study.

Temperatures recorded from January to March 1985 at the snow-soil interface were as low as -11°C, but were generally in the -1 to -5°C range. Air temperatures were -2 to -19°C but were known to be as low as -40°C.

Snow cover ranged from 40 to 77 cm.

*Anthelmintic trials in captive caribou*

Ivomec succeeded in eliminating patent infections of *Oesophagostomum, Ostertagia/Trichostrongylus, Capillaria* and *Trichuris.* Daily sampling of animals treated in September, 1985 revealed that feces were free of nematode eggs by three days post treatment. All other animals treated with Ivomec lost patent gastro-intestinal nematode infections by one week post treatment. A male calf treated during September 1985, continued to pass low numbers of *Nematodirus* spp. ova.

Trichostrongylid eggs were first detected in the feces by 26 to 251 days post treatment (Table 15). The lack of continual samples from some animals precluded exact determination of the date of new patent infections. Adult animals treated during the fall remained free of patent infections until winter. Animals treated during the spring generally acquired patent infections in fewer days than animals treated during fall. No nematodes were recovered at necropsy from one animal treated during April that died 19 days post treatment.

Table 15. Effect of Ivomec on the number of gastro-intestinal nematode ova passed in the feces of captive caribou.

| Date treated | Date patent | Days free[a] (min-max) | EPG[b] | |
|---|---|---|---|---|
| | | | PT | DP |
| Feb. 7/85 | Apr. 18/85 | 64-70 | 79 | 5 |
| Jul. 17/85 | Mar. 26/86 | 224-251 | 63 | 13 |
| Sep. 18/85 | Oct. 23/85 | 19-34 | 7672 | 371 |
| | Dec. 11/85 | 71-85 | 639 | 7 |
| | Dec. 11/85 | 78-85 | 130 | 37 |
| | Jan. 15/86 | 108-115 | 183 | 32 |
| Oct. 22/85 | Feb. 5/86 | 93-105 | 258 | 20 |
| Oct. 30/85 | Jan. 22/86 | 78-83 | 181 | 4 |
| Nov. 30/85 | Jan. 8/86 | 12-39 | 346 | 5 |
| Apr. 18/86 | May 14/86 | 6-26 | 95 | 19 |
| | Jun. 4/86 | 34-47 | 174 | 4 |
| | Jun. 4/86 | 41-47 | 194 | 13 |
| | Jul. 7/86 | 41-70 | 42 | 23 |
| | Jul. 9/86 | 41-72 | 219 | 10 |
| | Aug. 10/86 | 62-104 | 272 | 796 |

[a] Days free refers to minimum and maximum number of days that the animal was free of a patent infection. Min= last day no eggs were passed in feces, Max= first day eggs detected in feces after treatment.

[b] EPG= *Ostertagia/Trichostrongylus* eggs/g of dry feces prior to treatment (PT) and when first patent infection was detected (DP)

*Helminths recovered from wild and captive moose*

Samples from 19 wild moose were examined. These included five fecal samples, 11 duodenums and 14 abomasums with associated feces, and three duodenums without feces (Table 16). Samples were examined from all months except January, February, April and June. Eggs, adults, or immature stages of *Nematodirella alcidis* were recovered in 18 of 19 samples during all months sampled. Up to 562 worms were recovered from one moose, however, intensity was generally low (111±54). Immature worms (inhibited $L_4$ or sub-adults) were usually more numerous than mature adults (Table 16). *Nematodirella alcidis* were occasionally recovered in the abomasum.

Few eggs of *N. alcidis* were recovered from moose feces examined. Positive egg counts ranged from 1 to 43 EPG but generally were less than 10 (Table 16). No Lesions attributable to helminths were observed in any moose examined.

Inhibited fourth-stage *N. alcidis* average 3.62 mm (3.2-4.0) in length and possess a caudal spine. Twelve cuticular ridges are present near the base of the esophagus and are continuous to the anus. The cephalic vesicle ranges from 75-98 $\mu$m in length.

Eggs of *Monezia* sp. were recovered in the feces of one wild moose collected in November 1984. No other species of gastro-intestinal helminth was detected by flotation or at necropsy.

Captive moose passed eggs of *Capillaria* sp., *Trichuris* sp., *Monezia* sp., *Oesophagostomum* sp., *Ostertagia/Trichostrongylus* and *Nematodirus odocoilei* (Table 2). Fecal egg counts of captive moose were lowest during the winter months (Fig. 18). Peak egg counts of *Ostertagia/Trichostrongylus* occurred during the fall and were 220 and 290 EPG. The adult moose passed more eggs

Table 16. Intensity of *Nematodirella alcidis* infection in moose of Northwestern Ontario.

| Date | Sex | Age | EPG[a] | Mature | Immature[b] |
|---|---|---|---|---|---|
| Mar. /86 | M | 2+ | 43 | -[c] | - |
| May. /86 | - | - | 13 | - | |
| | - | | 9 | | |
| | - | - | 7 | - | - |
| May. /85 | M | 5+ | 1 | 9 | 26 |
| Jul. /84 | M | 5+ | 0 | 0 | 5 |
| Aug. /85 | F | <1 | | P[d] | P |
| | F | 1+ | - | 142 | 420 |
| Sep. /84 | F | <1 | 2 | - | - |
| Oct. /84 | M | 1+ | 18 | 1 | 0 |
| | F | 2+ | 1 | 1 | 0 |
| | M | 1+ | 1 | 20 | 40 |
| | M | 3+ | 0 | 0 | 0 |
| | M | 5+ | 0 | 0 | 4 |
| Oct. /85 | F | 2+ | - | 7 | 30 |
| Nov. /84 | M | 1+ | 21 | 3 | 0 |
| Dec. /84 | F | 3+ | 0 | 0 | 11 |
| | M | 1+ | 0 | 1 | 190 |
| | M | 8+ | 21 | 101 | 315 |

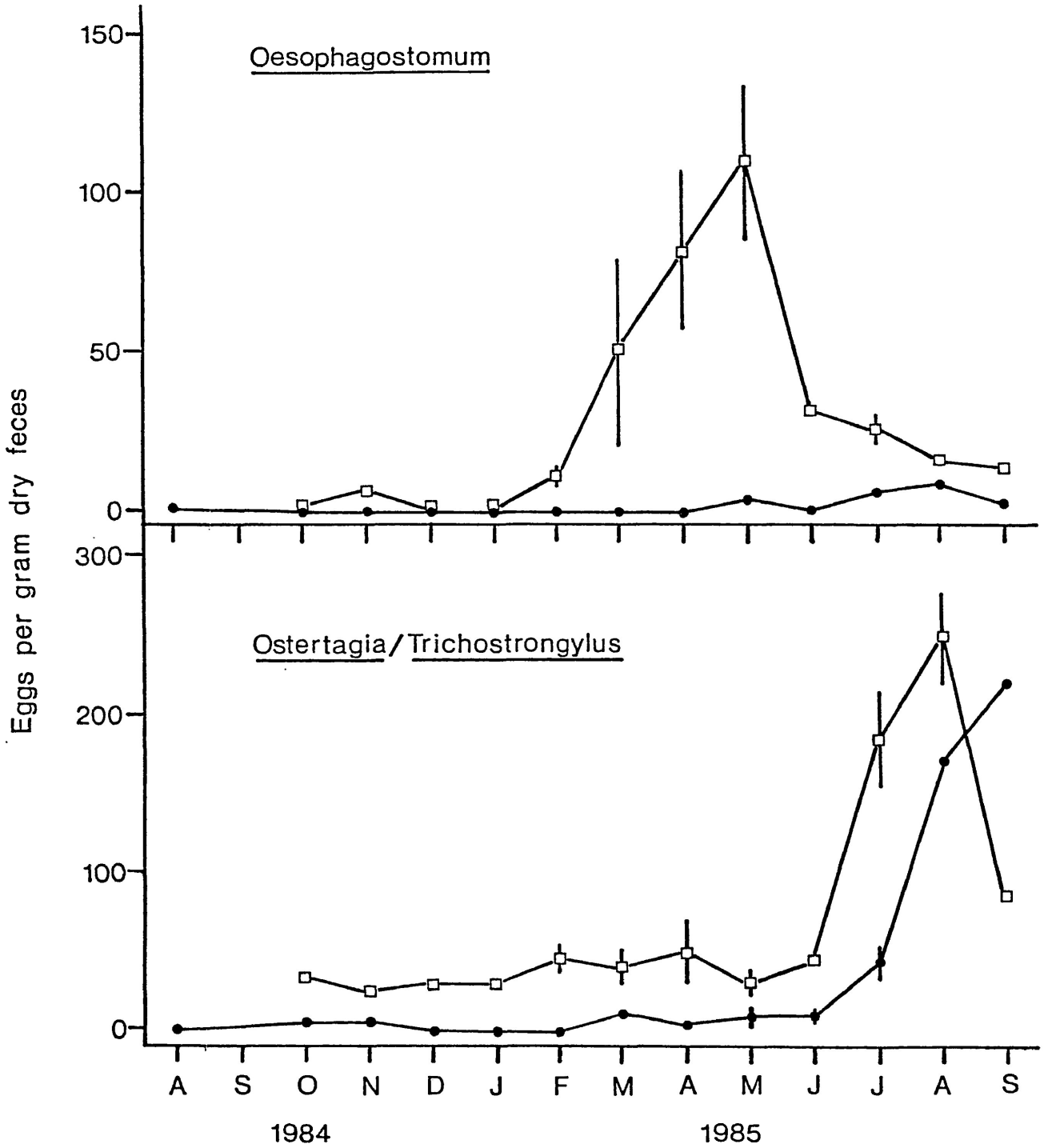
[a] Eggs/g of dry feces.

[b] Immature worms include females that were not gravid and males without spicules as well as fourth stage larvae.

[c] Feces or duodenum not examined.

[d] Present but not counted.

Fig. 18. Seasonal changes in the monthly mean number of nematode ova (EPG) passed in the feces of captive moose. (calf ● ; adult □ ).


Oesophagostomum
Ostertagia/Trichostrongylus
Eggs per gram dry feces
150
100
50
0
300
200
100
0
A S O N D J F M A M J J A S
1984
1985

of *Oesophagostomum* in her feces than the calf. Ova of *N. odocoilei* were first detected in the feces of the calf and adult moose during October and November 1984 respectively. Eggs were regularly recovered until the beginning of April (Adult) and the end of May 1985 (calf). The calf moose sporadically passed eggs of *N. odocoilei* until September 1985, at which time she was removed from the farm. Maximum egg counts of *N. odocoilei* were 144 and 11 EPG for the adult and calf respectively. *Oesophagostomum* egg counts ranged from 1 to 7 and 5 to 172 EPG for the calf and adult moose respectively (Fig. 18). Eggs of *Trichuris* were regularly recovered from both moose throughout the study.

## DISCUSSION

Fifteen species of Trichostrongyloidea representing seven genera were recovered from wild and captive caribou examined in this study. A total of 28 species (10 genera) have been reported from *Rangifer* in the past (Table 17). *Ostertagia gruhneri*, *O. arctica*, *Nematodirella longissimespiculata*, *Nematodirus tarandi* and *Dictyocaulus viviparus* are known from *Rangifer* throughout their holarctic distribution and are the most common species reported.

Generally, wild caribou are hosts to fewer species of parasites than domestic reindeer. Cross transmission of parasites between domestic and wild ungulates and *Rangifer* appears to be common. Captive caribou acquired numerous species from other ungulates present at the Kakabeka Falls Game Farm.

*Teladorsagia circumcincta* and its minor forms (see Lancaster et al. 1983) are generally thought to be parasites of domestic sheep (*Ovis aries*) (see Dunn 1978). Becklund and Senger (1967) reported the bighorn sheep (*Ovis canadensis*) as a common host of *T. circumcincta* and *T. trifurcata.* However, the genus is common in caribou of Canada. *Teladorsagia circumcincta* has also been reported from mule deer (*Odocoileus hemionus*) by Jenson et al. (1982) and Taber and Dasmann (1958), and from muskoxen (*Ovibos moschatus*) by Gibbs and Tener (1958). The scarcity of this genus in wild cervids of central and eastern North America may be due to the absence of wild sheep in this area.

The most common species of Nematodirinae reported from caribou and reindeer are *Nematodirella longissimespiculata* and *Nematodirus tarandi* (=*Nematodirus skrjabini*) (Table 17). *Nematodirella longissimespiculata* has also been reported from muskoxen (*Ovibos moschatus*) by Samuel and Gray (1974)

Table 17. Review of selected references on Trichostrongyloidea parasitizing caribou and reindeer.

| Species | Host[a] | Source[b] |
|---|---|---|
| *Ostertagia gruhneri* | R | 1,2,3 |
| | WWC,CWC | 4, This study. |
| *O. arctica* | R | 3 |
| | WWC,CWC | this study |
| *O. leptospicularis* | R,CWC | 5,6,7, this study |
| *O. kolchida* | R,CWC | 7, this study |
| *O. mossi* | WWC | 4 |
| *O. occidentalis* | R | 1 |
| *O. ostertagi* | R,CWC | 3,5, this study |
| *O. lyrata* | R | 1,3,5 |
| *Ostertagia* sp. | R | 5,8,11,12 |
| | WWC | 9,10,13 |
| *Teladorsagia circumcincta* | R | 1,5 |
| | WWC,BGC | 10, this study |
| *T. trifurcata* | R | 1 |
| | BGC,WWC | 14,10,15 |
| *T. davtiani* | R | 3 |
| *Marshallagia marshalli* | R | 1 |
| *Spiculopteragia spiculoptera* | R,CWC | 5, this study |
| *S. alcis* | R | 5,6 |
| *S. boehmi* | R | 7 |
| *S. assymetrica* | CWC | this study |
| *S. dagestanica* | R | 3 |
| *Trichostrongylus axei* | R,CWC | 3, this study |
| *T. probuluris* | R | 3 |
| *T. colubriformis* | R | 3 |
| *T. vitrinus* | R,CWC | 3, this study |
| *Haemonchus* sp. | R | 3 |
| *Cooperia punctata* | R | 3 |
| *C. pectinata* | R | 3 |
| *Nematodirella longissimespiculata* | R | 2,3,4,11,16,17 |
| | WWC,CWC | 4,10,13, this study |
| *Nematodirella* sp. | R | 12 |
| *Nematodirus tarandi* | R | 3,8,16, |
| | WWC | 13 |
| | BGC | this study |
| *N. filicollis* | WWC | 4 |
| *Nematodirus* sp. | R | 12 |
| | WWC | 10 |
| *Dictyoculus viviparous* | R | 3,8,12,18 |
| | WWC,CWC | 4,10,15,19, this study |

Hosts include reindeer (R), wild woodland caribou (WWC), captive woodland caribou (CWC) and barren-ground caribou (BGC).

[b] Sources include: 1, Bye and Halvorsen 1983 (Svalbard); 2, Leader Williams 1980 (South Georgia); 3, Pryadko 1976 (USSR); 4, Bergerud 1971 (Newfoundland, Canada); 5, Rehbinder and Christensson 1977 (Sweden); 6, Rehbinder and von Szokolay 1978 (Sweden); 7, Borgsteede 1982 (Sweden); 8, Hadwen 1922b (Alaska, U.S.A.); 9, Cowan 1951 (British Columbia, Canada); 10, Low 1976 (British Columbia, Canada); 11, Clausen et al. 1980 (Greenland); 12, Kummeneje 1980 (Greenland); 13, Hout and Beaulieu 1984 (Quebec, Canada); 14, Choquette et al. 1957 (Northwest Territories, Canada); 15, Jean et al. 1982 (Quebec, Canada); 16, Shalaeva 1972 (USSR); 17, Thing and Clausen 1980 (Greenland); 18, Christensson and Rehbinder 1975 (Sweden).

and *N. tarandi* has been recovered in roe deer (*Capreolus capreolus*) by Nilsson (1971). Bergerud's (1971) report of *Nematodirus filicollis* in caribou of Newfoundland may be incorrect. Ova of *Nematodirus odocoilei* were detected in the feces of caribou from the Topsails herd, Newfoundland and adult worms were recovered in a captive caribou calf captured in Newfoundland. The ova and males of these two species are similar. Unfortunately, Bergerud (1971) did not deposit museum specimens. *Nematodirus odocoilei* is a common parasite of white-tailed deer (Prestwood and Pursglove 1981) and mule deer (Becklund and Walker 1967a). Walker and Becklund (1970) examined reports of *N. filicollis* from white-tailed deer and determined that all specimens were actually *N. odocoilei.*

*Dictyocaulus viviparus* (=*Dictyocaulus eckerti*) is a cosmopolitan parasite of ungulates (Skrjabin et al. 1954). This species is known to infect domestic cattle (Dunn 1978), and all species of native North American cervids (Dikmans 1938).

Eggs of *Capillaria* sp. were commonly observed in the feces of caribou from northwestern Ontario and Newfoundland. The genus has been reported from *Rangifer* in Sweden (Christensson and Rehbinder 1975; Rehbinder and Christensson 1977) and the Soviet Union (Pryadko 1976). *Capillaria* sp. is commonly reported from white-tailed deer in the United States (Prestwood and Pursglove 1981) and is known from muskoxen (Samuel and Gray 1974).

This appears to be the first report of *Trichuris* sp. from caribou of North America. The genus is known from reindeer of the Soviet Union (Pryadko 1976). Eggs of *Trichuris* were commonly observed in the feces of Topsails animals but rarely from caribou of northwestern Ontario. *Trichuris* sp. is known from all other species of cervids native to North America

(Taber and Dasmann 1958; Prestwood and Pursglove 1981; Stock and Barrett 1983; Lankester 1984).

Reports of *Monezia* are common in *Rangifer* of North America (Hadwen 1922a; Erickson and Highby 1942; Low 1976; this study), Europe (Christensson and Rehbinder 1975; Rehbinder and Christensson 1977), Svalbard (Bye 1985), the Soviet Union (Shalaeva 1972; Pryadko 1976) and South Georgia (Leader-Williams 1980). The two species commonly reported include *M. benedini* and *M. expansa.* White-tailed deer (Foreyt and Samuel 1979), mule deer (Jensen et al. 1982) and moose (Lankester 1984) have been reported as hosts of *M. benedini.*

*Setaria yehi*, which was recovered from caribou of the Slate Islands, is the only species of *Setaria* found in North American cervids (Hibler and Prestwood 1981). It is known from white-tailed deer, mule deer and moose (Hibler and Prestwood 1981). This genus has been reported from caribou and reindeer in North America (Erickson and Highby 1942; Dieterich and Luick 1971; Dieterich 1980; this study), Norway (Kummeneje 1980) and the Soviet Union (Pryadko 1976). *Skrjabinema* sp. has been reported from reindeer in South Georgia (Leader-Williams 1980) and the Soviet Union (Pryadko 1976), and caribou of Canada (Cowan 1951; this study).

Some helminths formerly considered parasites of *Odocoileus* spp. of North America now appear to be firmly established in caribou. These include *N. odocoilei* (present study), *Ostertagia mossi* (see Bergerud 1971), *Parelaphostrongylus odocoilei* (see Gray and Samuel 1986), *Fascioloides magna* and *Parelaphostrongylus andersoni* (Lankester unpublished). These reports do not appear to represent incidental infections, but suggest caribou are suitable hosts and that these parasites are transmitted in the absence of white-tailed

deer. The presence of several white-tailed deer parasites in caribou of Labrador and Newfoundland may indicate that caribou once shared range with white-tailed deer in these areas.

Nine species of gastro-intestinal nematodes recovered in this study from captive caribou are also known from a variety of wild and domestic ungulates. *Nematodirus helvetianus, Trichostrongylus* spp. and *Oesophagostomum venulosum* are common parasites of domestic cattle (Dunn 1978). *Nematodirus helvetianus* has been reported in muskoxen and wapiti (*Cervus elaphus*) of North America (Samuel and Gray 1974; Webster and Rowell 1980; Stock and Barrett 1983). *Oesophagostomum venulosum* has been reported from moose (Lankester 1984), white-tailed deer (Prestwood and Pursglove 1981) and mule deer (Brown 1961) of North America. *Trichostrongylus axei* is known from wapiti in Alberta (Stock and Barrett 1983) and white-tailed deer (Prestwood and Pursglove 1981). Both species of *Trichostrongylus* recovered from captive caribou in this study have been reported from *Rangifer* in the Soviet Union (Pryadko 1976). *Spiculopteragia assymetrica, S. spiculoptera, O. leptospicularis* and *O. kolchida* are known from fallow deer (Drozdz 1965) which were probably the source of infection for captive caribou. *Ostertagia kolchida* was recently reported from North America for the first time (Rickard and Zimmerman 1986). Only small numbers (<1200 (1-3%)) of *Ostertagia ostertagi* were recovered in captive caribou. This species is commonly found in domestic cattle (Dunn 1978) and appears to exhibit some degree of host specificity. Williams (1987) reported low rates of establishment in experimentally infected goats. McGhee (1981) found that *O. ostertagi* would not infect healthy white-tailed deer fawns. Conti and Howerth (1987) estimated 1793 *Ostertagia ostertagi* to be present in a white-tailed deer

suffering from a heavy tick infestation.

*Nematodirus tarandi* was originally described from reindeer of Alaska by Hadwen (1922b) and has been reported from reindeer in the Soviet Union (Shalaeva 1972), caribou in Quebec (Hout and Beaulieu 1984) and roe deer in Europe (Nilsson 1971). Mitskevich (1929) described *Nematodirus skrjabini*, from reindeer in the Soviet Union. This species is morphologically similar to *N. tarandi* and was regarded as its synonym by Dikmans (1936). Skrjabin et al. (1954) disagreed with this synonymy and suggested that *Nematodirus tarandi* was a member of the genus *Nematodirella.* A comparison of specimens of *N. tarandi* deposited by Hadwen (1922b) with the description provided by Mitskevich (1929) supports the synonymy suggested by Dikmans (1936). The lack of drawings in the original description of *N. tarandi* may have contributed to the confusion of the two species. The drawings of Mitskevich (1929) do not illustrate the tip of each dorsal ray as bifid. All specimens examined in this study possess dorsal rays with bifid tips, typical of the genus.

The discrepancy between the length of the type specimens and those examined in the present study might be explained by host age. The body length of *Nematodirus* sp. is variable and may depend on the age or immune status of the host (Smith 1970). No record of host age was given for type specimens, however, based on the small size of the worms, it is likely that the worms were recovered from an adult caribou.

Until recently, it has been difficult to identify females of the Nematodirinae to species. However, studies by Lichtenfels and Pilitt (1983 a,b) of the synlophe of *Nematodirella* and *Nematodirus* have made it possible to pair males and females of one species based on the number and arrangement of cuticular ridges. As a result, the specific identification of eggs becomes

possible.

Within the Nematodirinae, evolution of the synlophe (longitudinal cuticular ridges) is thought to have proceeded with an increase in the number of ridges along with a reduction in their height (Lichtenfels and Pilitt 1983 a,b; Durette-Desset 1985). Studies on the synlophe of *Nematodirus* of domestic ruminants have shown that the typical number of ridges present at the base of the esophagus is 14-18 (Lichtenfels and Pilitt 1983b). Both *N. tarandi* and *N. odocoilei* possess 38-42 ridges at the base of the esophagus, far higher than reported for any other species. The large number of ridges imply that *N. tarandi* and *N. odocoilei* are highly evolved members of the genus. Lichtenfels and Pilitt (1983a) examined specimens of *Nematodirella* from North American ruminants and suggested that *N. longissimespiculata* from caribou is one of the most evolved species in that genus. These data suggest that the Nematodirinae parasitizing cervids, particularly *Rangifer*, are more highly evolved than those in bovids.

Diagnostic features of the family Trichostrongylidae are usually characters with a large degree of variability. The family is in need of a more adequate description than that presently provided by Durette-Desset (1983). The subfamily Ostertagiinae is distinguished by the absence of a prominent buccal capsule, the parallel nature of rays 2 and 3 and a short dorsal ray. Despite previous efforts by authors attempting to classify the genera within the subfamily Ostertagiinae, confusion still exists with respect to the validity of some genera. Recent works by Durette-Desset (1983), Gibbons and Khalil (1982), and Drozdz (1965) have placed 5, 17 and 18 genera, respectively, within the subfamily. Of these genera, five are shared by the classification schemes of all three authors. These include *Ostertagia, Teladorsagia, Marshallagia,*

*Longistrongylus* and *Spiculopteragia* (the only valid genera according to Durette-Desset (1983)). For the purpose of this discussion and parsimonious reasons, the classification of Durette-Desset (1983) is followed. Terms used to describe anatomical features of the bursa and genital cone follow Durette-Desset (1983).

Suitable, discrete characters for separation of the genera within the Ostertagiinae include the morphology of the dorsal and ventral processes of the spicules, the form of the dorsal ray and the arrangement of the bursal rays. The genus *Ostertagia* has spicules with either one or both lateral processes ending in barbs, *Teladorsagia* have simple points on the processes and *Spiculopteragia* have complex spicule tips with fan-like membranes. The dorsal ray is also diagnostic of these genera. *Ostertagia* and *Teladorsagia* have dorsal rays arising from the outer base of the externodorsal ray, while in *Spiculopteragia* the dorsal ray arises from within the bursa.

Durette-Desset (1982) suggested that the Ostertagiinae arose from two genera, *Graphidium* and *Hyostrongylus.* Based on the arrangement of the bursal rays, she argued that the genera *Ostertagia, Marshallagia* and *Longistrongylus* arose from *Graphidium*, while *Teladorsagia* and *Spiculopteragia* were derived from *Hyostrongylus.* However, a close examination of the bursa, spicules and cervical papillae of *Ostertagia*, *Teladorsagia*, and *Spiculopteragia* suggest that *Ostertagia* and *Teladorsagia* are more similar morphologically than are *Teladorsagia* and *Spiculopteragia.* *Teladorsagia* is not widely accepted as a distinct genus and has been synonymized with *Ostertagia* by Lancaster et al. (1983).

Recent studies have shown that polymorphism among the Ostertagiinae is common, and that up to three forms of one biological species may occur

(Lancaster et al. 1983). Known polymorphic systems include *Teladorsagia circumcincta/trifurcata/davtiani, Ostertagia ostertagi/lyrata* and *Ostertagia leptospicularis/kolchida* (Lancaster et al. 1983). These discoveries suggest that characteristics previously used to separate genera and species are not as useful as was once thought. Prior to the classification system proposed by Durette-Desset (1983), a polymorphic species could have representatives spanning two genera (*Ostertagia-Teladorsagia, Ostertagia-Skrjabinagia*). Polymorphic species occur as major and minor forms (ranked by numerical dominance) and can be distinguished by the following criteria: the minor form never occurs in the absence of the major form, minor forms have thicker spicules and are always present as a small percentage of the major form (Lancaster et al. 1983). *Ostertagia gruhneri* and *Ostertagia arctica*, two abomasal nematodes recovered from caribou in this study, satisfy all the above criteria with *O. gruhneri* and *O. arctica* being the major and minor forms respectively.

Drozdz (1971) examined the genus *Skrjabinagia* and suggested that there were nine valid species within the genus. The genus was distinguished by the presence of Sjoberg's organ and the form of the spicules. These characters appear to be unique to the minor forms of polymorphic *Ostertagia* sp. In an earlier paper, Drozdz (1965) recognized that members of *Skrjabinagia* occur in small numbers compared to the species with which it was associated. This appears to be the first hint that species previously placed in *Skrjabinagia* might be minor forms of polymorphic pairs in the genus *Ostertagia* as suggested Lancaster and Hong (1981).

The similarity of the minor forms of *Ostertagia* spp. compared with the wide degree of variability in the morphology of the major forms, suggest that the minor forms may be similar to the ancestral *Ostertagia.* Sjoberg's organ

and spicules with pointed heels may be ancestral characters. Durrete-Desset (1985) discussed characteristics of the bursa and suggested that an elongated dorsal ray was an ancestral characteristic. Both *O. arctica* and *O. kolchida* have dorsal rays longer than their respective major forms, supporting the hypothesis that these forms are more primitive than either *O. gruhneri* or *O. leptospicularis* morphotypes.

*Teladorsagia trifurcata* and *T. davtiani* are known polymorphs of *T. circumcinta* (Lancaster et al. 1983). The first two are readily separated by the form of Sjoberg's organ, but are otherwise indistinguishable (Rose 1962). Neither of the minor forms of *T. circumcincta* was recovered from Beverly caribou. This may have been due to the small number of *T. circumcinta* recovered (less than two in any animal), thus reducing the probability of recovering the minor forms which usually occur as less than 10% of the adult male population.

The recent discovery of polymorphism indicates that a re-evaluation of characters (eg. length of dorsal ray in Gibbons and Khalil (1982)) used to separate genera and species is needed. The search for suitable characters to define species within the subfamily will no doubt be a difficult one. Further work should evaluate the degree to which polymorphism occurs within the subfamily using the methods of Lancaster *et al.* (1983) or by examining the ratios of suspected minor forms to their companion species. *Ostertagia mossi* and *O. dikmansi* from white-tailed deer appear to be ideal candidates as a polymorphic pair. If valid genera are to be separated based on discrete characters, and are to form natural groupings without exception, the use of bursal ray arrangement and spicule tip morphology are the only characters that offer a true dichotomy useful in separating genera within the Ostertagiinae.

The average number of abomasal nematodes recovered from various caribou herds examined in this study appears to be related to herd density. The most heavily parasitized animals were from the Slate Islands while those from the Beverly herd harbored the fewest worms. Studies in the southeastern United States have demonstrated that the average intensity of infection with abomasal nematodes in white-tailed deer increases with increasing herd density (Eve and Kellogg 1977). These workers suggested that an abomasal parasite count (APC) in excess of 1500 indicated that white-tailed deer of the southeast had exceeded their carrying capacity. Abomasal parasite counts have since been used as an indicator of range utilization and overcrowding. The mean number of abomasal nematodes recovered from Slate Islands caribou during the spring and fall was 4230. Using the criteria described for white-tailed deer by Eve and Kellogg (1977), Slate Islands caribou would be considered as existing above the carrying capacity of the Islands.

The intensities of infection with abomasal nematodes found in caribou of the Slate Islands fall within the range reported for other caribou and reindeer herds. Hout and Beaulieu (1984) reported mean APC's of approximately 2200 (580-6172) in lactating George River caribou during the fall. Bye and Halvorsen (1983) recorded a mean APC greater than 10000 for adult Svalbard reindeer examined during October. Leader-Williams (1980) estimated that there were 2200 abomasal nematodes present in one animal examined during the summer from South Georgia. Seasonal studies on abomasal nematodes in reindeer from Sweden have shown that adults harbored a mean of 900 abomasal nematodes during the winter (Rehbinder and von Szokolay 1978) and had moderate to low infections during the fall (Rehbinder and Christensson 1977).

One male examined during the winter from the Slate Islands harbored 1600 adult abomasal nematodes, within the range reported by Rehbinder and von Szokolay (1978). The presence of large numbers of inhibited larvae in the abomasa of several animals from the Slate Islands may indicate that worm burdens in the spring could approach 10000.

The relatively high APC's reported for island dwelling *Rangifer* may be due to the high densities that these animals occasionally attain when marooned on islands in the absence of predators. Svalbard reindeer exist at a density of 3.3 per $km^2$ (Bye and Halvorsen 1983), similar to those found on Pic and Otter Islands. Reindeer on South Georgia occur at densities of 40 to 80 per $km^2$ (Leader-Williams 1980), higher than found on the Slate Islands. It is unfortunate that Leader-Williams examined only one animal from South Georgia. Foreyt and Samuel (1979) noted that white-tailed deer living in a predator-free enclosure acquired more abomasal nematodes than deer living at lower densities outside the enclosure.

Changes in feeding habits caused by overcrowding may increase the transmission and acquisition of trichostrongyles. Early studies on the food habits of Slate Islands caribou reported that the summer diet consisted of deciduous shrubs, herbs and lichens (Cringan 1957). These studies were conducted when caribou densities were thought to be low ($1.1/km^2$). More recent studies have shown that caribou on the Slate Islands have had a significant impact on the vegetation and are reducing preferred browse species (Anon. 1986). Large amounts of sand and gravel were frequently found in the abomasa of caribou examined from the Slate Islands, suggesting that ground feeding was common. Subsequently, caribou grazing closer to the ground are more likely to acquire large numbers of infective abomasal nematode larvae.

Foreyt and Samuel (1979) noted that white-tailed deer grazing close to the ground harbored more worms than deer that browsed.

It is likely that the criteria of >1500 abomasal nematodes suggested as indicative of overcrowding in white-tailed deer (Eve and Kellogg 1977) may may not be applicable to caribou. Most studies on caribou report mean APC's in excess of 2000 without any evidence of disease or overcrowding. Due to their larger body size, caribou might have an increased tolerance for higher numbers of abomasal nematodes than white-tailed deer. Differences in the biology and habitat requirements of the subspecies of *Rangifer* make the estimation of an overall APC indicative of overcrowding difficult. Woodland caribou in northern Ontario exist at much lower densities ($<0.1/km^2$) than observed in insular herds (Anon. 1985). Barren ground caribou of the Kaminuriak herd exist as localized high density groups ($25/km^2$), but are constantly moving and covering large areas resulting in an overall low density ($<0.3/km^2$) for their range (Parker 1972).

Abomasal parasite counts reported from white-tailed deer are generally lower than those found in woodland caribou of the Slate Islands. Baker and Anderson (1975) estimated a maximum mean APC of 2300 during late summer in white-tailed deer of Ontario. Only four of 47 animals had APC's greater than 3000 (maximum=4068) (Baker 1974). Demarais et al. (1983) found up to 4034 abomasal nematodes in white-tailed deer of Mississippi, however, median counts never exceeded 2200 worms. Mean APC's of less than 2000 have been reported in white-tailed deer from New Jersey and Oklahoma (Pursglove 1977), Maryland and Virginia (Davidson and Crow 1983), Texas (Waid et al. 1985), Kentucky (Davidson et al. 1985) and the southeastern United States (Couvillion et al. 1982). A common feature of abomasal nematode infections in white-tailed deer

of the United States is the large number of species parasitizing the deer.

Reports of APC's from other wild ungulates are also generally lower than found in *Rangifer*. Studies on fallow deer and sika deer living sympatrically with white-tailed deer report mean APC's of 752 and 928 respectively (Davidson et al. 1985; Davidson and Crow 1983). Moose in North America are rarely infected with abomasal nematodes. Low prevalence (<15%) and intensity (1-3) have been reported from Alberta (Samuel et al. 1976; Stock and Barrett (1983), while none were observed in northwestern Ontario (present study). Low prevalence and intensities were found in wapiti examined from Alberta (Stock and Barrett 1983). Muskoxen do not appear to harbour large numbers of abomasal nematodes. Samuel and Gray (1974) reported a prevalence of 21% and a mean egg count of 7 EPG based on fecal examination of wild muskoxen from Alaska, the Northwest Territories and Norway.

It is generally thought that younger animals are more susceptible to parasitism than older animals (Gibbs 1973). Young cattle are known to harbour heavy burdens of abomasal nematodes (>100000) after their first fall on pasture (Martin et al. 1957; Smith and Archibald 1968a,b; Pott et al. 1978). Examination of animals from the Slate Islands indicated that calves had fewer worms than adults (Lankester unpublished; present study). No worms were recovered from one barren-ground caribou calf examined during the winter while adults harbored a mean of 388 abomasal nematodes. Other studies have also reported low numbers of abomasal nematodes in caribou calves (Rehbinder and von Szokolay 1978; Bye and Halvorsen 1983; Hout and Beaulieu 1984). White-tailed deer fawns in Ontario had fewer adult worms than adult deer collected during July and August (Baker and Anderson 1975). In contrast, fawns from Mississippi generally harbored more abomasal nematodes than did

adults (Demarais et al. 1983).

Fecal egg counts from caribou calves were higher than those from adults. A similar observation was reported by Leader-Williams (1980). One might conclude from this that calves harbour more worms than adults during the late summer and early fall. However, other explanations are possible. Lower volumes of feces passed by calves may result in the concentration of ova. The higher fecundity of female worms in calves may also increase egg counts.

Immunity to trichostrongyles may be expressed in several ways (Michel et al. 1971). Hosts may effectively control worm numbers by preventing the establishment of infective larvae or by periodically expelling adult worms (Connan 1976). They may also affect the morphology of the worms by causing stunting (Ross 1963), reducing fecundity (Michel 1963; Smith 1970; Taylor and Thomas 1986) and altering the percentage of worms with vulval flaps (Hong et al. 1986). Generally, young animals tend to have less immunity to trichostrongyles than older animals which have been previously infected.

Host age and herd density had a significant affect on the immune response against abomasal nematodes recovered from wild caribou. Caribou calves from the Slate Islands tended to have larger and more fecund females worms than adults. Worms recovered from Beverly caribou were longer than those recovered from adults from the Slate Islands. The lower intensity of infection with *O. gruhneri* in Beverly caribou may explain the presence of larger worms in these animals. Resistance to *O. ostertagi* in cattle is slow to develop and related to the number of worms present in the animal (Michel 1963).

The similarity of fecal egg counts from Slate, Pic and Pukaskwa herds might then be explained by the presence of fewer but more fecund worms in

the Pic Island and Pukaskwa animals. It would be of considerable interest to obtain worms from Beverly caribou during the summer or fall to determine if the fecundity of female *Ostertagia* is comparable to that observed in Slate Islands calves. In cattle, the level of egg production of *O. ostertagi* is similar regardless of the total number of worms, and appears to be regulated by the host (Michel 1969). Although fecal egg counts do not appear to be useful for estimating the level of infection in individual animals, they are of value in demonstrating the seasonal fluctuation of prevalence and intensity within individual herds.

The absence of vulval flaps in female Ostertagiinae is thought to be related to the immune status and previous experience of the host (Denham 1969; Michel et al. 1972; Hong et al. 1986). The proportion of female *O. gruhneri* with vulval flaps from Slate Islands calves (73%) and Beverly caribou (77%) was larger than from Slate Islands adults (10%). If the immune response that inhibits the development of the vulval flap is an acquired one, it is likely that caribou of the Beverly herd are not as heavily parasitized as caribou on the Slate Islands. One caribou examined from Pic Island harbored female *Ostertagia* with 43% vulval flaps and 32.5 shelled eggs in utero. Measurements of total body lengths of male and female worms were not different from those observed in Beverly caribou. These data suggest that caribou on Pic Island do not harbour as many worms as those on the Slate Islands, and may have levels of infection comparable to Beverly caribou.

Immune responses against trichostrongyles may also be affected by the physiological state of the host. Brunsden (1962b) was able to demonstrate that poorly fed sheep harbored more worms than well fed animals. Caribou dying in captivity supplied further evidence of the effects of stress as a factor in

disease. A common feature of captive animals that died with signs of ostertagiasis was the history of nutritional and physical stress. The large proportion of female *Ostertagia* spp. with vulval flaps in all captive animals suggest that they were immunologically compromised and not capable of controlling worm burdens as well as healthy animals. Conti and Howerth (1987) reported ostertagiasis in a white-tailed deer stressed by a heavy tick infection. Genchi et al. (1986) noted that beef cattle experiencing transport stress exhibited a marked rise in fecal egg counts. The maturation of large numbers of inhibited larvae as a result of stress were thought responsible for the continued rise in egg counts after relocation.

Clinical and subclinical aspects of disease caused by *Ostertagia* sp. are well recognized in domestic animals. Two types of ostertagiasis have been defined (Armour 1970). Type I ostertagiasis generally occurs during summer and fall as the result of acquisition of large numbers of infective larvae accumulating on pasture. These larvae complete their development in the gastric glands by three weeks post ingestion. Type II ostertagiasis generally occurs from March to May (Armour 1970) but may be seen at other times of the year when induced by environmental stress of any type (Jubb et al. 1985). Maturation of large numbers of inhibited larvae which have persisted in the host over winter are the primary cause of type II ostertagiasis in cattle (Armour 1970). Signs of type I and type II ostertagiasis include emaciation, inappetance, anemia and a profuse, watery diarrhoea. The lesions produced by both types of disease are essentially similar when viewed macroscopically (Jubb et al. 1985), but may differ histologically (Snider et al. 1983). Subclinical signs include poor weight gain, poor wool production and reduced milk production by lactating animals (Gibbs 1982).

The disease observed in captive caribou during 1986 was probably type I ostertagiasis caused by *O. leptospicularis*. No diarrhoea was observed in any animal at the time of death, however, clinical signs of inappetance and unthriftiness were evident. The elevated fecal egg counts observed are also diagnostic of this type of disease (Armour 1970). Pathological changes to the abomasum of captive caribou were similar to those reported for domestic animals with heavy infections of *Ostertagia ostertagi* (Jubb et al. 1985). The lesions observed in wild caribou do not resemble those caused by the emergence of immature worms, but are similar to lesions caused by adult worms in close association with the mucosa (Dunn 1978). Similar lesions have been described in white-tailed deer (Prestwood et al. 1973).

It would appear that in caribou, abomasal worm burdens in excess of 20000 abomasal nematodes are required to cause weight loss and death. The data indicate that egg counts (and probably worm burdens) rise rapidly, possibly after a certain threshold of weight loss has been reached. In cattle, rises in fecal egg counts due to poor condition have also been observed (Michel 1969). This may have important implications for herd health and calf survival after exceedingly severe winters. The combination of high caribou density and low food availability in the late winter on the Slate Islands may predispose caribou, especially calves, to periodic outbreaks of ostertagiasis during late winter and early spring. Bye and Halvorsen (1983) recorded maximum APC's of 21000 nematodes in Svalbard reindeer that appeared to be in poor condition.

Levels of infection with *N. longissimespiculata* in caribou of the Slate Islands are high compared with those reported elsewhere. Leader-Williams (1980) reported a prevalence of less than 10% and intensities of less than 20

worms in reindeer on South Georgia. Fecal egg counts were 1 EPG in all positive samples. In contrast, Slate Islands caribou harbored up to 1220 worms, with mean egg counts generally above 150 EPG during the fall. Barren-ground caribou of the Beverly herd and caribou of the Slate Islands passed similar numbers of eggs in their feces during March.

Little is known of the pathogenicity of *N. longissimespiculata.* Although *Nematodirella* does not generally occur in domestic ruminants, *Nematodirus* commonly infects cattle and sheep. Large numbers of *Nematodirus* (>10000) are required to cause disease in domestic animals (Jubb et al. 1985). Such worm burdens were not observed in wild caribou suggesting that *N. longissimespiculata* does not approach pathogenic numbers.

The low incidence of patent infections of *N. longissimespiculata* in Beverly caribou during December may be a result of competition with *N. tarandi* at that time. The upper duodenum appears to be the preferred location of both species. Kass and Bergstrom (1983) noted that *Nematodirella* was displaced to the posterior portion of the intestine when found concurrently with *Nematodirus.* Experimental studies have demonstrated that the presence of one species can inhibit or prolong the development of another. Alghali et al. (1985) demonstrated that concurrent infections of *Nematospiroides dubius* and *Hymenolepus citelli* in mice resulted in a decreased growth rate and longer lifespan of the tapeworm. Mapes and Coop (1970) showed that the presence of *H. contortus* in experimentally infected lambs could slow the maturation of large numbers of *N. battus.* Further studies demonstrated that concurrent infections with *Haemonchus* resulted in fewer, smaller and less fecund *Nematodirus* compared with controls (Mapes and Coop 1971). *Haemonchus* was thought to affect *Nematodirus* by altering conditions

in the intestine.

Data from the Slate Islands and the Northwest Territories clearly demonstrate the ability of caribou to resist reinfection with Nematodirinae as yearlings and mature adults. It is well documented in domestic animals that *Nematodirus* generally infects only young animals. Cattle and sheep develop a well marked immunity to this genus after an initial infection and normally remain refractory to reinfection in later years (Brunsden 1962a; Smith and Archibald 1968a). Hadwen (1922a) and Hout and Beaulieu (1984) suggested that the prevalence of Nematodirinae was high in caribou calves, but did not give actual numbers. Although different species of *Nematodirus* were involved in captive caribou, the same phenomenon was observed. In the present study, males tended to be more susceptible to infection with *Nematodirella* than females during the fall. This suggests that the stress of the rut may compromise the immunity acquired earlier in life. Higher APC's in males have been noted during the rut in reindeer (Bye and Halvorsen 1983) and white-tailed deer (Demarais et al. 1983).

Adult muskoxen and moose do not appear to be able to resist reinfection with Nematodirinae. Samuel and Gray (1974) detected ova of *Nematodirella* and *Nematodirus* in 70% of muskoxen feces examined during June and July. In the present study, 96% of moose were infected with *Nematodirella alcidis*, compared with less than 20% of caribou infected with *N. longissimespiculata.* The high prevalence in moose might be a result of the low numbers of worms that moose harbour. A continuous infection with a small number of worms may not be sufficient to induce an immune response capable of preventing reinfection in older animals.

Limited observations suggested that wild caribou calves were more

susceptible to infection with *Dictyocaulus viviparus* than adults. Similar results have been reported in domestic animals (Michel 1969; Jubb et al. 1985). The levels of infection with *D. viviparus* observed in wild caribou do not appear to be pathogenic, suggesting that this worm is not a potential problem on the Slate Islands. Occasional instances of serious infection in reindeer calves have been noted in Norway (Kummeneje 1977), and are commonly associated with acute pneumonia caused by *Pasteurella multocida* (Kummeneje 1980). Studies on the free-living stages of *Dictyocaulus* indicate that this genus is more susceptible to dessication and freezing temperatures than are other trichostrongylid nematodes (Rose 1956). The apparent susceptibility of *Dictyocaulus* larvae to extreme environmental conditions may prevent the establishment of pathogenic numbers in wild caribou of the Slate Islands.

Caribou also appear to be able to effectively prevent reinfection with *Trichuris* sp.. Captive adult caribou did not pass trichurid eggs in their feces. Eggs of Trichuris were only detected in the feces of Topsails caribou infected with *Nematodirella* and *Nematodirus*, parasites usually restricted to calves. The presence of *Trichuris* eggs in the feces of the captive calf and adult moose suggests that moose do not develop an immunity to this worm. Lower fecal egg counts of *Oe. venulosum* may also reflect an increased resistance with age (Goldberg 1951). Captive adult caribou passed fewer eggs in their feces than calves. An apparent immune response against *Monezia* sp. has been noted in reindeer (Bye 1985) and moose (Samuel et al. 1976). In the present study, results appear to be conflicting. Barren-ground caribou do not retain patent infections of *Monezia* after 2 years of age, however, calves on the Slate Islands rarely demonstrated patent infections with *Monezia* while typical ova were detected in 26% of feces from adults. Both captive calves and adults

were infected with *Monezia.*

Seasonal fluctuations in prevalence and intensity may be caused by the absence of suitable vectors (*Monezia*) or infective stages (Trichostrongyles, *Capillaria*) at particular times of the year. The longevity of the parasite and factors associated with transmission may also influence the seasonality of infection. *Paramphistomum* spp. are known to halt egg production during winter and resume production when environmental conditions become suitable for transmission (Snider 1985). Inhibited larvae and lowered fecundity of adult females appear to be two mechanisms used by *O. gruhneri* to survive over the winter months. It is not clear whether reduced fecundity in female *Ostertagia* during the winter is caused by senility, a host immune response, or a response to environmental conditions. The similar fecundity observed during the winter months regardless of host age would tend to rule out an immune related cause.

Seasonal fluctuations in fecal egg counts of abomasal nematodes similar to those observed in the present study have been reported in reindeer (Leader-Williams 1980), muskoxen (Samuel and Gray 1974), cattle (Pott et al. 1978) and sheep (Ayalew and Gibbs 1973; Rose et al. 1984). Studies on sheep in Greenland (Rose et al. 1984) and cattle in England (Pott et al. 1978) have also shown peaks in fecal egg counts during the fall. Generally, peak egg counts coincide with the presence of large numbers of adult worms, which are known to fluctuate seasonally in cattle (Malczewski 1970).

Dramatic increases in fecal egg counts during the spring (spring rise) are common in sheep and cattle, and are usually attributed to the maturation of large numbers of inhibited larvae that overwinter in the abomasum (Gibbs 1967). The presence of inhibited larvae and the spring rise are thought to be a mechanism ensuring survival of worms in environments where free-living

stages do not readily persist (Gibbs 1973). A distinct spring rise in fecal egg counts similar to that observed in cattle and sheep by other workers was not evident in caribou.

Anthelmintic studies demonstrated that infections of *Ostertagia* sp. could be acquired as late as November but not during the winter (February to March). Calves appear to acquire patent infections during their first few weeks of life.

*Nematodirella longissimespiculata* also demonstrated seasonal change in prevalence and the number of eggs passed in the feces. The absence of patent infections during the spring and early summer is probably due to the lack of susceptible animals (calves) rather than some seasonal aspect of the worm's biology.

Seasonal fluctuations in the prevalence of *Monezia* and *Capillaria* were also evident. Bye (1985) noted that *Monezia benedini* was most prevalent in reindeer during the fall. Samuel and Gray (1974) reported peak prevalence of *Monezia* in wild muskoxen during June. The absence of *Capillaria* in Beverly caribou may indicate that environmental conditions for this parasite are not suitable in these regions. Samuel and Gray (1974) did not detect ova of *Capillaria* in wild muskoxen although they were present in the feces of captive animals that shared range with other species.

The free-living stages of *Ostertagia gruhneri* do not survive freezing as well as those of *N. longissimespiculata.* Eggs of *Ostertagia* frozen for short periods were not capable of hatching, suggesting that the drop in fecal egg counts during the winter months may be in response to environmental conditions. Female *O. gruhneri* laying eggs during the winter months would reduce their fitness. Jasmer et al. (1986) noted that *T. circumcinta* was able

to overwinter as an egg, however these results were based on freezing at -18°C for only 15 hours. Eggs of *N. longissimespiculata* were capable of hatching after 11 months at -18°C, far longer than would be experienced under natural conditions. Although no experiments were conducted on eggs of *Nematodirus tarandi*, casual observations suggested that this species is also capable of withstanding prolonged periods of freezing as an egg. Other studies have also demonstrated that under field conditions, the free living stages of the Nematodirinae are longer lived than those of the abomasal nematodes (Smith and Archibald 1969; Smith 1972; Slocombe 1974). Boag and Thomas (1985) noted that infective *Ostertagia* spp. larvae held at 5 to 30°C survived longer than those of *Nematodirus* spp.. Under natural conditions, the free living stages are subjected to freezing and dessication. The results of the present study suggest that the free-living stages of *O. gruhneri* and *N. longissimespiculata* behave in a similar fashion to their counterparts in domestic ruminants.

Other differences in the biology of gastro-intestinal helminths were evident. *Nematodirella longissimespiculata* does not appear to over-winter within the host as an inhibited larva. This may represent an adaptation by the worm to the strong immune response which generally precludes reinfection of caribou. In contrast, inhibited *N. alcidis* were commonly found in moose regardless of season. *Nematodirella* eggs passed in the winter months are capable of infecting caribou during the ensuing grazing season, while those of *Ostertagia* are not likely to survive.

The poor development of *Nematodirus* spp. and *Nematodirella* spp. eggs in feces has been noted for other species of *Nematodirus* (Herlich 1954; Baxter 1959). Rose (1966) demonstrated that the hatching of *N. helvetianus* is highly

dependent on temperature. Eggs of *Nematodirus battus* require large amounts of free water for development (Parkin 1976) and may need to be incorporated within the soil before large numbers will develop. In contrast, eggs of *Ostertagia* sp. readily hatch in feces (Levine 1980). The relationship between temperature and day of first hatch observed for *N. longissimespiculata* are similar to those of *N. helvetianus* (Herlich 1954). The lack of development at 3°C may indicate a low temperature threshold at which little or no development can occur. This was noted by Herlich (1954) for *N. helvetianus.*

Ash and Atkinson (1983) noted that in order for larvae of *N. battus* to hatch, a period of chilling was required after the infective stage had been reached. No such requirement was observed for *N. longissimespiculata.* The requirement of chilling in *N. battus* has been suggested as a mechanism ensuring synchronous hatching of large numbers of infective larvae during the spring (Parkin 1976).

This appears to be the first report of inhibited *Ostertagia gruhneri* recovered from caribou. Hout and Beaulieu (1984) noted small numbers (10-170) of inhibited *Ostertagia* sp. in George River caribou. Leader-Williams (1980) reported immature worms in reindeer of South Georgia, however no specific details on the state of development were reported. Rehbinder and von Szokolay (1978) found no inhibited larvae in the abomasa of reindeer bulls examined during the fall. Baker and Anderson (1975), reported inhibited *Ostertagia* sp. (*O. mossi* or *S. odocoilei*) from white-tailed deer of Ontario.

The phenomena of inhibition (arrested development) is common among trichostrongyles and has been reviewed by Michel (1974) and Schad (1977). Inhibited forms generally are most numerous during the winter months (Michel 1974) but may be present at other times of the year when environmental

conditions are not suitable for the survival of the free living stages (Vercruysse 1983). Several mechanisms have been suggested that may control the onset of inhibition. These include age of infective larvae (Stockdale et al. 1970), response to environmental conditions (Armour et al. 1969) and host immune status (Martin et al. 1957).

The success of Ivomec in removing patent infections of gastro-intestinal nematodes in the present study was not unexpected. Early anthelmintics were not successful in removing inhibited forms (Michel 1969). The present study supports the observations of other workers that Ivomec can eliminate inhibited stages (Yazwinski et al. 1981; Armour et al. 1980; Egerton et al. 1981). The rapid drop of fecal egg counts observed in animals treated during the fall months has also been noted in animals treated with oxfendazole (Ogunsusi 1979). Ivomec appears to have some residual effect as indicated by the prolonged period between treatment and the onset of patent infections during fall trials. Most animals did not pass eggs of *Ostertagia* sp. for several weeks after the expected prepatent period of 18-21 days. The apparent resistance of *Nematodirus* sp. to the effects of Ivomec (Eysker 1986) and several other anthelmintics (Hoberg et al. 1985) has been reported.

*Moose parasites*

All species recovered in the present examination of wild and captive moose have been reported previously in this host with the exception of *N. odocoilei*. *Nematodirella alcidis*, the only gastro-intestinal nematode recovered from wild moose in the present study has been reported in moose of Canada (Threfall 1967; Samuel et al. 1976; Stock and Barrett 1983), the United States (Olsen and Fenstermacher 1942), Sweden (Nilsson 1971) and Finland (Drozdz

and Bylund 1970). Few studies have reported the actual level of infection with this parasite, however most suggest that the intensity of infection is relatively low. Olsen and Fenstermacher (1942) noted that some pathological changes to the small intestine were evident in heavy infections. No other study has reported the predominance of immature stages of *N. alcidis*. Arrested development has been reported among the Nematodirinae for *Nematodirus filicollis* (Nilsson 1971) and *Nematodirus abnormalis* (Beveridge et al. 1985). It is noteworthy that few immature *N. longissimespiculata* were recovered in caribou. *Nematodirella alcidis* generally has a high prevalence and does not appear to be restricted to young animals as is *N. longissimespiculata* of caribou. Reports of prevalence range from 47% (Olsen and Fenstermacher 1942) to 100% (Threfall 1967, Nilsson 1971).

The large proportion of inhibited *N. alcidis* larvae found in wild moose may serve as a reservoir of parasites allowing for year round dissemination of eggs. Arrested development in *Nematodirella alcidis* does not appear to be in response to environmental conditions or the immune status of the host. Moose are generally infected with a low number of worms and do not demonstrate any apparent age related immunity. Continuous dissemination of eggs may increase the chances of moose coming in contact with infective stages in spite of their habit of browsing which is not conducive to the acquisition of large numbers of trichostrongyles. Watkins and Fernando, (1986) have suggested that inhibited *Obelescoides cuniculi* act as a reservoir to replenish adult worms that are lost.

*Oesophagostomum, Trichuris* and *Monezia* have all been reported from moose of North America (Olsen and Fenstermacher 1942; Samuel et al. 1976; Stock and Barrett 1983). *Capillaria* has been recorded from moose of Sweden

(Nilsson 1971). *Trichuris* is known to cause disease in captive moose (Nilsson 1971).

Abomasal nematodes (Ostertagiinae) have been reported in moose of Canada, however intensity and prevalence tend to be low (Samuel et al. 1976; Stock and Barrett 1983). Nilsson (1971) reported 100% prevalence of abomasal nematodes in moose of Sweden as did Drozdz and Bylund (1970) for moose of Finland. In contrast to these findings, no abomasal nematodes or their ova were recovered from wild moose that were examined in Ontario. Captive moose passed low numbers of eggs of abomasal nematodes throughout the year. *Haemonchus contortus* and *T. axei* have both been reported in moose of Sweden (Nilsson 1971). *Haemonchus contortus, O. ostertagi* and *T. axei* are common parasites of cattle and sheep and were probably acquired from domestic animals sharing range with captive moose.

The apparent absence of abomasal nematodes in wild moose and the relatively low fecal egg counts in captive moose would tend to suggest that moose are not as susceptible to infection with these nematodes as caribou. The presence of large numbers of *Ostertagia* sp. in wild caribou indicates that conditions suitable for successful transmission of abomasal nematodes exist in northwestern Ontario. Because moose tend to browse more than caribou, the opportunity to become infected may not be readily available. Captive moose were regularly seen grazing at the game farm. Other studies on moose of Canada support the findings that moose are rarely infected with abomasal nematodes.

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Appendix 1. Sample size and number of calf, adult male and adult female woodland caribou fecal samples collected from the Slate Islands from 1975 to 1986. Unknown animals are those classified as adult pellets (Appendix 2) but not to sex, others include samples that could not be classified to age due to their amorphic nature or the lack of adequate data on calf and adult pellet weights at these times.

| | | | Adult | | | |
|---|---|---|---|---|---|---|
| Date | n | calf | male | female | unknown | other |
| Oct. 75 | 12 | 2 | 5 | 4 | 1 | 0 |
| Jul. 78 | 10 | 1 | 0 | 5 | 4 | 0 |
| Sep. 78 | 26 | 5 | 8 | 7 | 0 | 6 |
| Sep. 80 | 12 | 0 | 3 | 0 | 0 | 9 |
| Oct. 80 | 13 | 5 | 2 | 6 | 0 | 0 |
| Aug. 84 | 20 | 0 | 0 | 0 | 0 | 20 |
| Sep. 84 | 10 | 0 | 0 | 0 | 0 | 10 |
| Oct. 84 | 10 | 0 | 0 | 0 | 0 | 10 |
| Mar. 85 | 36 | 0 | 0 | 0 | 0 | 36 |
| Apr. 85 | 8 | 0 | 0 | 0 | 0 | 8 |
| May. 85 | 33 | 0 | 0 | 0 | 0 | 33 |
| Jun. 85 | 33 | 0 | 0 | 0 | 0 | 33 |
| Jul. 85 | 53 | 1 | 0 | 0 | 40 | 12 |
| Aug. 85 | 34 | 2 | 0 | 0 | 21 | 11 |
| Sep. 85 | 35 | 5 | 2 | 10 | 15 | 2 |
| Oct. 85 | 23 | 4 | 0 | 2 | 16 | 1 |
| Mar/ Apr. 86 | 29 | 0 | 0 | 0 | 0 | 29 |
| May. 86 | 5 | 0 | 0 | 0 | 0 | 5 |
| Jun. 86 | 24 | 2 | 0 | 6 | 0 | 16 |
| Total | 426 | 27 | 20 | 40 | 97 | 241 |

Appendix 2. Mean weight (g) of oven dryed fecal pellets collected from wild and captive caribou from July 1985 to June 1986.

| | Calf | | Adult | |
|---|---|---|---|---|
| Month | Wild | Captive | Wild | Captive |
| Jul. | 0.11 | 0.06 | 0.23 | |
| Aug. | 0.135 | 0.08 | 0.23 | |
| Sep. | 0.084 | 0.09 | 0.22 | |
| Oct. | 0.131 | 0.11 | 0.26 | |
| Nov. | | 0.13 | | |
| Dec. | | 0.13 | | |
| Jan. | | 0.12 | | 0.16 |
| Feb. | | 0.12 | | 0.16 |
| Mar. | | 0.103 | | 0.147 |
| Apr. | | 0.105 | | 0.157 |
| May | | 0.10 | | 0.11 |
| Jun. | | | 0.22 | |

Appendix 3. F values for comparison of sample means of body length, spicule length and female fecundity of *Ostertagia gruhneri* by host age and season. Abbreviations include Slate Calf (SC), Slate Adult (SA), Pic Adult (PA) and adult Barren-ground Caribou (BGC). Seasons include winter (W), fall (F) and Spring (S).

| | Male length | Spicule length | Female length |
|---|---|---|---|
| SC-SA | 264.4 (1,311) | 337.5 (1,311) | 474.5 (1,312) |
| SC-BGC | 8.6 (1,179) | 0.3 (1,179) | 23.0 (1,203) |
| SC-PA | 3.4 (1,108) | 42.7 (1,108) | 12.5 (1,118) |
| SA-BGC | 199.7 (1,332) | 150.3 (1,332) | 378.1 (1,337) |
| SA-PA | 78.2 (1,261) | 40.1 (1,261) | 108.0 (1,252) |
| PA-BGC | 0.1 (1,129) | 3.7 (1,129) | 0.5 (1,147) |

F (1,60;p=0.05)=4.0, F (1,120;p=0.05)=3.92, F (1, ;p=0.05)=3.84

Fecundity by season, location and host age.

| | | | |
|---|---|---|---|
| SA(F)-SC(F) | 219.6 (1,192) | SA(F)-PA(F) | 55.5 (1,162) |
| SA(F)-SA(W) | 46.6 (1,192) | SA(F)-SA(S) | 1.5 (1,162) |
| SA(W)-SC(W) | 0.4 (1,88) | SA(W)-BGC(W) | 1.2 (1,175) |
| SA(W)-SA(S) | 18.1 (1,88) | SC(W)-BGC(W) | 0.1 (1,145) |
| SC(W)-SC(F) | 133.9 (1,88) | SC(F)-PA(F) | 18.8 (1,88) |