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Factors Affecting the Distribution and Transmission of *Elaphostrongylus rangiferi* in Caribou (*Rangifer tarandus caribou*) of Newfoundland

By

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Abstract

Elaphostrongylus rangiferi is an introduced parasite in caribou (*Rangifer tarandus caribou*) of Newfoundland and has caused at least two epizootics of cerebrospinal elaphostrongylosis (CSE), a debilitating, neurologic disease. To understand the conditions necessary for such outbreaks, two hypotheses were investigated. First, I examined whether parasite abundance was primarily determined by herd density or climatic conditions. The abundance of *E. rangiferi* was represented by counts of first-stage larvae in feces of calves and yearlings collected in February from nine distinct caribou herds in Newfoundland. Seven of the nine herds had concomitant infections of *E. rangiferi* and another protostrongylid nematode, *Parelaphostrongylus andersoni*. The Cape Shore and Bay de Verde caribou had only *P. andersoni*. Abundance of *E. rangiferi* was highest among young animals (calves and yearlings) in the Avalon ($\bar{x}$ =632 ± 14) and St. Anthony ($\bar{x}$ =526 ± 145) herds during February. Reports of CSE were most frequent in these two herds. Abundance was correlated positively with mean annual minimum temperatures (r_s=0.829, df=6, P=0.04), and the number of days per year above 0°C (r_s=0.812, df=6, P=0.05) and negatively with mean summer temperatures (r_s= -0.830, df=6, P=0.04). Abundance was not correlated with herd density.

It was also hypothesized that young animals develop an immunity to *E. rangiferi* that prevents re-infection later in life. This was examined by pressing the brains of known-age caribou to detect recently acquired *E. rangiferi*. Worms were found on the brains of young caribou but not in animals older than two years, except for those of the Avalon herd. The continued infection of older animals in the Avalon herd may be due to lower immuno-competence of animals in a herd

only recently infected with *E. rangiferi*.

This study also examined the usefulness of abomasal parasite counts (APC) (Trichostrongyloidea) in predicting herd density. Three species of trichostrongylid nematodes were present: *Ostertagia gruhneri*, *Trichostrongylus axei* and *Haemonchus contortus*; *O. gruhneri* predominated. There was no significant correlation between mean APC and herd density (r_s= -0.40, df=4, P=0.60). However, further analysis indicated that worm burden was influenced by climate. APCs were positively correlated with mean annual temperatures (r_s= 1.0, df=4, P≤0.01), and annual rainfall (r_s= 1.0, df=4 P≤0.01) and negatively correlated with total annual snowfall (r_s= -1.0, df=4, P≤0.01). The highest APCs (up to 12,245 ± 2,470) were found in caribou of the two most southerly herds (Cape Shore and Avalon), and the lowest (2,513 ± 281) occurred in the most northerly herd (St. Anthony).

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Introduction

Elaphostrongylus rangiferi Mitskevich, 1958 is a common parasite of semi-domesticated and wild reindeer (*Rangifer tarandus tarandus*) in northern Fennoscandinavia and Russia. It is responsible for periodic epizootics of a debilitating neurologic disease seen particularly in young animals in late winter. An intense verminous pneumonia is also a consequence of infection (Roneus and Nordkvist 1962; Polyanskaya 1963; Nordkvist 1971). Historically, considerable economic loss has occurred during epizootics in the reindeer industry due to winter deaths, unthriftiness, forced culling for slaughter, and carcass trimming (Lankester 2000). Goats and sheep kept on reindeer pasture also develop neurologic signs (Bakken and Sparboe 1973; Handeland 1991; Handeland and Sparboe 1991), as do moose infected experimentally (Lankester 1977; Stéen et al. 1997). Currently, the impact of *E. rangiferi* on the reindeer industry in Fennoscandinavia has been diminished by the widespread use of ivermectin (A. Oksanen pers. comm). This method of control is precluded, however, for use in wild cervids such as caribou (*R. t. caribou*) in Newfoundland, Canada where *E. rangiferi* has been introduced.

In 1908, 300 reindeer purchased by Sir Wilfred Grenfell were shipped from the Altenfjord region of Norway and landed near St. Anthony at the northern tip of Newfoundland (Lankester and Fong 1989). Fifty of these animals were taken over-land to the central part of the Province and were corralled near the town of Buchans for several months before being returned to St. Anthony where a growing herd was held for at least 10 years. This history of reindeer movement and accounts of some escaping to join native caribou, convincingly explains the presence of *E. rangiferi* in caribou of Newfoundland. The parasite is now established in almost all of the caribou herds on the island (70,000 animals total) but spread only recently to an isolated herd on the

southern Avalon Peninsula in the early 1990's (Lankester and Fong 1998). Despite repeated importations of reindeer from Norway to North America and translocations of reindeer and caribou from Newfoundland to mainland Canada and the United States, there is no evidence that the parasite has become established elsewhere other than in caribou of Newfoundland (Lankester and Fong 1989).

E. rangiferi is a slender, dark brown nematode found on the surface of skeletal muscles especially beneath the shoulders, on the chest and belly, and in the hind limbs (Roenus and Nordkvist 1962; Lankester and Northcott 1979). Specimens can also be found in the cranium within 90 days of infection (Hemmingsen et al. 1993). In this location, infecting third-stage larvae, acquired by ingesting gastropods, develop to the fifth stage on the surface of the brain before exiting along cranial and lateral spinal nerves to mature among muscles. Gravid females in muscle fascia deposit eggs that are carried by the venous system to the lungs where they become lodged in alveolar capillaries. Eggs hatch and first-stage dorsal-spined larvae are brought to the pharynx by the bronchial escalator, swallowed and passed in fecal pellets about 120 days after initial infection (Handeland et al. 1994). First-stage larvae penetrate the foot of terrestrial gastropods where development to the infective stage occurs in 75 days at 12 °C (Halverson and Skorping 1982). In Newfoundland, the slug *Deroceras laeve*, is the primary intermediate host for *E. rangiferi* (Lankester and Fong 1998).

The severity of elaphostrongylosis appears to be dose-dependent (Halverson 1986b). Animals acquiring relatively few worms may show no outward signs of disease and only experience a sub-clinical verminous pneumonia. Those ingesting moderate numbers of the parasite will often separate from the herd, stay in one place for an extended period and appear "stunned"

or unusually tame. Reindeer and caribou acquiring the heaviest infections, will show distinct neurologic signs including unsteady gait, walking in circles, hindquarter weakness, or an inability to stand (Roneus and Nordkvist 1962; Polyanskaya 1963; Nordkvist 1971; Handeland and Norberg 1992; Lankester 2000). This most severe manifestation of the disease is known as cerebrospinal elaphostrongylosis (CSE) and is seen most frequently from January to March, but may be observed at any time of the year.

Periodically, an unusually large number of caribou exhibit CSE. Two epizootics have been reported since the recognition of the parasite on the island. The first occurred in the Buchans and Gaff Topsails areas of central Newfoundland in the early to mid-1980's (Lankester and Fong 1989). During this period, large numbers of calves and yearlings showed severe signs of the disease. Older animals were not involved. In 1995, an outbreak occurred on the Avalon Peninsula. The parasite had only recently infected this herd and over the ensuing 3 years, the Avalon Caribou herd declined from an estimated 7,000 animals to less than 2,500 (Lankester and Fong 1998). CSE was observed in calves and yearlings but also in adult animals.

Conditions responsible for epizootics of CSE have been examined by Handeland and Slettbakk (1994) in reindeer raised in northern Norway above 69 °N where long-term mean summer temperatures (June - August) were 11.9 °C. Seven late winter outbreaks seen over a 33 year period were highly associated with high temperatures and moderately associated with heavy rainfall during the preceding summer. High summer temperatures were also associated with outbreaks of CSE in goats pastured with reindeer during the same reporting period (Handeland and Slettbakk 1995). Above average summer temperatures were thought to induce the mass development of infective *E. rangiferi* larvae in gastropods leading to heavier than usual infections.

Intuitively, host density should be an important factor in determining parasite abundance. However, tests of this assumption in wild host populations are often weakened by the difficulties in obtaining reliable estimates of density. Aerial surveys traditionally have been the method of choice for determining the size and range of ungulate populations but these are costly and generally produce estimates with wide confidence limits (Timmermann 1993; Thomas 1996). Additionally, the particular habits of caribou, being gregarious nomads that segregate seasonally by age and sex and that follow sporadically changing migration paths, make it especially difficult to estimate density in relation to actual range utilization. In the present study, caribou densities determined by aerial survey were available for analyses (Mahoney 2000) but an effort was made to derive independent estimates that might better reflect the seasonal densities of animals and their repeated use of range considered to be important in parasite transmission.

An indirect method of determining cervid densities using parasites was tested by Eve and Kellogg (1977). These authors used counts of non-pathogenic nematodes in the abomasum as an index of white-tailed deer population densities over 13 states in the southeastern United States. Deer in good body condition and in habitats with only light browsing, had low abomasal parasite counts (APCs). In contrast, deer in poor condition in areas showing heavy browsing, had high APCs. Populations considered to be approaching carrying capacity had intermediate counts. In their study, carrying capacity was defined as the maximum number of deer that an area could support without deterioration of herd health or habitat quality. Eve and Kellogg (1977) stressed that APCs did not provide a measure of deer density per unit area of land but instead, reflected how closely deer numbers approached the capacity of the habitat to maintain a healthy population.

Parasite numbers were affected not only by the density of deer and the quality of the habitat but by the nutritional plane of animals in the host population and their ability to maintain an effective immunological defense against heavy infections. Poorly nourished deer have more worms that, in turn, pass more eggs onto the range and increase chances for infection of other poorly nourished deer. Bye (1987) assessed APCs in a study of wild and semi-domesticated reindeer at 3 locations in the mountain tundra region of south Norway. Reindeer at the site with highest density (2.5 animals/ km^2) had the greatest mean intensity of abomasal worms and were in poorest condition.

The presence of *E. rangiferi* in several discrete herds separated latitudinally provided an opportunity to test the hypotheses that parasite abundance is affected by herd density and climate. As well, the presence of *E. rangiferi* in the Avalon herd for only 8 years compared to 90 years for the other herds made it possible to test the hypothesis that the susceptibility of caribou to infection is related to their history of association with the parasite. Measuring the level of *E. rangiferi* infection in caribou of Newfoundland was, however confounded by the presence of *Parelaphostrongylus andersoni*, a related protostrongylid nematode with a similar dorsal-spined larva (Lankester and Hauta 1989; Lankester and Fong 1998). Although this parasite produces a verminous pneumonia, it is not neurotropic. Also, it has a shorter prepatent period (as short as 51 vs.120 days) and larvae of shorter mean length than those of *E. rangiferi*.

Study herds and climate

Woodland caribou were examined from 9 discrete herds in Newfoundland (Fig. 1).They experienced a variety of climatic conditions and occupied seven different eco-regions of the Province (Meades and Moores 1994).

Study Herds

The St. Anthony herd

This herd is located near the tip of the Great Northern Peninsula in an area classified as the Strait of Belle Isle Ecoregion with arctic-alpine vegetation and limited forests of white spruce and balsam fir occurring as krummholz. In 1998, the St. Anthony herd was estimated to contain 8,405 caribou existing at a density of 2.0 animals/ km^2 (Table 1). In winter, the herd remains close to the eastern shore extending from Pistolet Bay, south toward Pigeon Cove, and west to Seal Bay. The spring distribution overlaps somewhat with the winter range, but animals remain inland and tend to move east toward the town of Roddickton.

The Northern Peninsula herd

This herd is located in the central part of the Great Northern Peninsula in an area classified as the Northern Peninsula Ecoregion. Forested areas consist mainly of balsam fir except at high elevations where black spruce is the main component. Bog and shrub forest are also typical of this region. In 1998 this herd was estimated at 2,729 individuals and a density of 0.6 animals/km^2.

The Gros Morne herd

This herd is located in the southwestern part of the Great Northern Peninsula including Gros Morne National Park and spans 3 ecoregions (Western Newfoundland, Northern Peninsula, and Long Range Mountains Ecoregions). The area is noted for its mountainous terrain reaching

Fig 1. Map of Newfoundland, Canada showing the areas occupied by the caribou herds from which hunter-killed caribou and fecal samples were collected: 1 - St. Anthony (51°N, 55°W); 2- Northern Peninsula (50°N, 55°W); 3- Gros Morne (49°N, 56° W); 4 - Gaff Topsails (49°N, 56° W); 5 - Middle Ridge (47°N, 53°W); 6 - Merasheen Island (47°N, 52°W); 7 - Avalon (46°N, 51°W); 8 - Cape Shore (46°N,51°W) and 9 -Bay de Verde (48° N, 51°W).

Table 1. Estimated size and density of Newfoundland caribou herds.

Herd	Location	Area Occupied (km^2)	Caribou observed †	Density (animals/km^2)
St. Anthony	51°N, 55°W	4,132*	8,405	2.0
Northern Peninsula	50°N, 55°W	4,640	2,729	0.6
Gros Morne	49°N, 56°W	3,960*	2,877	0.7
Gaff Topsails	49°N, 56°W	3,334**	5,980	1.8
Middle Ridge	47°N, 53°W	6,281*	19,765	3.0
Merasheen	47°N, 52°W	125	330	2.6
Avalon	46°N, 51°W	3,509**	1,845	0.5
Bay de Verde	48° N, 51°W	733**	102	0.1
Cape Shore	46°N, 51°W	590**	1,410	2.4

* 95% confidence limits of minimum convex polygon from telemetry recordings.
** Area of most extensive survey done.
†Mahoney (2000)

over 800 m above sea level. Vegetation on the highlands includes arctic-alpine plants and balsam forest. Lowlands to the west are dominated by bog and scrub forest with *Almus crispa* and *Salix spp*. The eastern foothills are forested with balsam fir and black spruce. The herd migrates seasonally between high and low elevations moving onto the highlands before calving in late May and remaining there until mid-October. At the highest altitudes, snow remains throughout the year providing a cool refuge for caribou, and limiting the number of insect pests that may disrupt feeding. The caribou move eastward into the foothills and lowlands in late October to early November; some move west toward the coast. In 1996, the Gros Morne herd was estimated at 2,877 individuals and a density of 0.7 animals/km^2. This has been considered one of the healthiest herds in Newfoundland.

The Gaff Topsails herd

This herd is located in central Newfoundland, south of the town of Badger in an upland region with several prominent peaks reaching 600 m above sea level. This area is situated in the Long Range Barrens Ecoregion characterized by barren lands dominated by *Kalmia angustifolia* and scarce forested areas. The summer season is short and cooler than other regions. Winter is typically long and cold. The vegetation is dominated by arctic-alpine plants aptly suited to the climate. Trees commonly occur as krummholz, consisting of eastern larch and black spruce.

The Gaff Topsails herd has a year-round distribution that covers approximately 3,400 km^2 and ranges in an area bounded by the Trans Canada Highway to the north and the Buchans Highway in the south. In the fall, caribou congregate around Goose Pond, south of the town of Howley. The winter distribution includes both the extreme east and west of the region. In the west, caribou aggregate around Goose Pond as they do in Autumn. In the east, they occupy a 500

km^2 area north of Millertown Junction. The calving ground is located south of Mt. Sheffield and is approximately 400 km^2. In 1989, this herd was estimated at 5,980 animals with a density of 1.8 animals/km^2.

The Middle Ridge herd

This herd is located in eastern Newfoundland, south of Gander. The area is classified as Central Newfoundland Ecoregion (Northcentral subregion) characterized by *Hylocomium*-balsam fir forest types and scrub heaths which are predominantly *Kalmia angustifolia*. The Middle Ridge experiences the warmest summers and coldest winters of any interior part of the island.

The range of the Middle Ridge herd extends south of the Northwest Gander River, between the Bay d'Espoir and Trans-Canada Highways, as far south as Gisborne Lake. In winter, caribou move toward the center of this area, between the Northwest Gander River and Tolt Mountain (1,076 m). In spring they occupy two areas to the north and south of the wintering grounds. In the north, the area is approximately 1,500 km^2 and located southeast of the Southwest Gander River. In the south they utilize a smaller area, approximately 750 km^2 located on the southeastern corner of the Bay de Nord Wilderness Reserve. High densities of woodland caribou are observed in the fall near Great Gull Lake along the Bay d'Espoir Highway and near the headwaters of Long Harbour River. The Middle Ridge herd was estimated in 1982 at 3,000 animals (Mahoney 2000). By 1995, the herd had reached 19,765 individuals and a density of 3.0 animals/km^2.

The Merasheen Island Herd

This herd is located on the Merasheen Island southwest of Arnold's Cove. The island is classified as belonging to the Southeastern Barren Ecoregion which is dominated by heathlands and limited forested areas. Vegetation is predominantly *Empetrum nigrum* and *Kalmia angustifolia*. Caribou are not native to Merasheen island. In 1962, several animals from the Middle Ridge herd were translocated to the Merasheen. The herd has since increased to an estimated 330 animals in 1998 and a density of 2.6 animals/ km^2.

The Avalon Peninsula Herd

This herd occupies an area in the southeastern part of the Avalon peninsula classified as the Hyper-Oceanic Barrens Ecoregion. The area is characterized by low expansive barrens dominated by *Kalmia angustifolia*, and forests limited to balsam fir krummholz. Several ground lichen species such as *Cladonia spp.* are abundant in this area. The Avalon range has a maritime climate of mild winters, cool summers, strong winds and high humidity. For the past several years, the Avalon herd has occupied an area in the extreme southeast of the peninsula. Animals range to the south of Peter's River, north to the tip of the Biscay Bay River and east to Cape Race (Con Finlay pers. comm.).

At the turn of the century, the Avalon herd was estimated at fewer than 100 animals (Bergerud, 1971). The population showed no sign of increase for many years. However, in a 12 year period beginning in 1967, the herd increased from 720 individuals to approximately 3,000 in 1979; an estimated density of 4 animals/km^2 (Bergerud et al. 1983). This increase was attributed to a number of factors, most importantly, the lack of calf predation by lynx (*Lynx canadensis*)

(Bergerud et al. 1983). By 1995, the herd had reached an estimated 7,000 individuals. Thereafter, numbers declined rapidly especially within the male cohort (Con Finlay pers. comm.). An epizootic of cerebralspinal elaphostrongylosis (CSE) caused by *Elaphostrongylus rangiferi* was seen in the Avalon herd from 1995-1998 and undoubtedly played a role (Lankester and Fong 1998). The population was estimated at 1,845 individuals in 1998 and a density of 0.5 animals/km^2.

The Cape Shore Herd

This herd is located on the southwest extension of the Avalon peninsula characterized as Maritime Barrens Ecoregion with limited forested areas composed of white birch and stunted balsam fir. *Empetrum nigrum* and *Kalmia angustifolia* are the dominant shrubs of this region. Human intervention had a definite impact on the pattern and shape of the landscape in this region. Indiscriminate fires set by early settlers and the railways in the 19th century contributed to the development of extensive heath lands. The caribou of the Cape Shore occupy a relatively small confined area and have no definite seasonal migrations.

Caribou were introduced to the Cape Shore in 1977 when, 28 animals (2 male and 4 female adults; 1 male and 13 female yearlings; 1 male and 6 female calves plus 1 unknown) were translocated from the nearby Avalon herd (Finlay and Oosenbrug 1984). The population increased steadily and was estimated at 184 animals in 1984. By 2000, the herd was estimated at 1,410 and a density 2.4 animals/km^2. Hunting was prohibited on the Cape Shore until 1998, when a resident-only hunt was permitted. The Cape Shore caribou herd includes a good proportion of large stags and no animals showing signs of CSE have been reported from this area.

The Bay de Verde herd

This herd is located on the northwest extension of the Avalon peninsula between Trinity Bay and Conception Bay and is classified as being in the Maritime Barrens Ecoregion (Northeastern subregion). This subregion is identified by its extensive forests consisting mainly of balsam fir. Caribou are new residents to this area. Thirty animals were translocated from the nearby Avalon herd in 1989. The range of the herd is located between Highways 80 and 70 to the west and east, respectively, and extends from the town of Old Perlican in the north to Highway 74 in the south. This herd was recently estimated at 102 individuals and a density of 0.1 animals/km^2.

Climate

Canadian Climatic Service weather data taken in proximity to the main caribou herds for the years 1997 and 1998 showed interesting differences in relation to latitude within Newfoundland (Table 2). The most southerly part of the island (46°N, 51°W) experienced the highest mean annual temperatures, lowest annual snowfall and highest precipitation. This region also had the greatest number of days with temperatures above 0°C, ranging from 305 days on the Avalon to 326 days on the Bay de Verde Peninsula. By comparison, the more northerly Gros Morne and Northern Peninsula herds (50°N, 55°W and 49°N, 56°W respectively) experienced about 60 fewer days with temperatures above 0°C, mean annual temperatures about 3°C lower and 150 cm more snow. These areas also were drier, receiving as little as 586 mm of rain at Gros Morne. An exception to the north-south climatic gradient was St. Anthony. This area, located at the most northerly point on the island, had a mean annual minimum temperature 2.5°C warmer and had approximately 15 more days with temperatures above 0°C than adjacent areas to the south.

Table 2. Canadian Climate Service weather data recorded in proximity to caribou herds in Newfoundland.

Herd[a]	Total[b] annual rainfall(mm)	Total annual snowfall(cm)	Total annual precipitation (mm)	Annual min. temp. °C	Annual max. temp.°C	Annual mean temp.°C	Mean no. days >0°C	Mean no. days >10°C
St. Anthony	960	240	1,200	0.5	6.8	2.5	275	117
Northern Peninsula	1,002	397	1,399	-2.0	6.6	2.8	262	147
Gros Morne	586	224	810	-2.0	6.5	2.2	259	141
Gaff Topsails	1,038	310	1,348	0.2	7.7	3.9	275	146
Middle Ridge	1,222	186	1,408	0.6	8.4	4.8	271	153
Merasheen	1,249	172	1,421	1.1	8.5	5.1	290	165
Avalon	1,293	145	1,438	1.2	8.8	5.4	305	155
Cape Shore	1,225	166	1,391	2.0	8.9	5.5	316	162
Bay de Verde	1,002	179	1,181	1.0	10.0	5.5	326	169

[a] Location of climatological station closest to the herd ranges were beginning in order from St Anthony: Flower's Cove (CCS Station #:8401583), Daniel's Harbour (8401400); Deer Lake/White Bay (8402069); Buchans (8400698), Grand Falls (8402050); Long Harbour (8402569); Heart's Content (8402080), St. Stephen's (8403618) and Cappahayden (8401070).
[b] Data are the mean of the years 1997 and 1998.

Methods

Samples from hunter- and road-killed caribou, collected from September 1998 to February 2000, included approximately 30 fecal pellets, the abomasum and the head including the jawbone. The entire central nervous system (CNS) and skeletal musculature were examined for *E. rangiferi* when road-killed and sick animals were collected. Animals were aged by tooth eruption and wear class pattern (Miller 1972). Sex, date of kill and location were recorded. Additional fecal pellets from approximately 30 animals were collected off the ground from each of the study sites in September, December and February of each year and from the more accessible Avalon herd almost every month. Pellets were placed in plastic sample bags taking care not to crush them before freezing. They were kept frozen for no more than 1 month before being thawed and examined at Lakehead University, Thunder Bay, ON.

Fecal examination and larval measurement

Thirty fecal pellets from each hunter-killed animal of known age were measured (length and width) using a digital micrometer. All fecal samples were examined for dorsal-spined, protostrongylid larvae using the modified Baermann beaker method (Forrester and Lankester 1997). Numbers of extracted larvae were expressed as larvae/g of dried fecal material. Mean length measurements of larvae were obtained by pooling all larvae recovered from individual fecal samples from a particular herd and randomly selecting 30 which were heat relaxed on a microscope slide and drawn and measured at 40x using a drawing tube in order to distinguish between *E. rangiferi* and *P. andersoni* (Lankester and Hauta 1989).

Herd density estimates and climate data

Density estimates for each herd were obtained from the Newfoundland Department of Forest Resources and Agrifoods (Mahoney 2000). Densities (animals/km^2) were derived using animal counts from aerial surveys and areas were estimated from actual area surveyed or from the seasonal movements of radio collared animals. Climate data were obtained from weather stations (Canadian Climate Service, Fredericton, NB.) located closest to the range of each herd studied and included mean annual temperature (maximum, minimum and mean), total annual snowfall, rainfall and total precipitation. Data also included the number of days per year above 0°C and above 10°C. Only data for the years 1997 and 1998 were considered. In addition, remote temperature recorders (HOBO data loggers, Hoskin Scientific, Burlington, ON) were placed on the ground and lightly covered with vegetation at locations on the range of each of the Middle Ridge, Gaff Topsails and St. Anthony herds from September 1999 to June 2000. On the range of the Avalon herd near Trepassey, NF one recorder was positioned on the ground and another was positioned 2 cm below surface vegetation.

Detecting recent *E. rangiferi* infection

Heads from known-age, hunter-killed caribou were examined for recently acquired *E. rangiferi* which can be found migrating in the pia-arachnoid covering the brain. The skull cap was removed using a bone saw, the brain removed and cranium and brain surface inspected visually. The location of any nematodes was recorded and grossly visible inflammation noted. Worms were counted and fixed in 70% alcohol with 10% glycerin for later examination. The brain was placed in a plastic sample bag, and frozen. It was later partially thawed and the outer surface tissue (1

cm deep), including the pia-arachnoid, was removed with a sharp scalpel, pressed between two heavy glass plates (4.5 x 4.5 cm) and examined for worms using a stereomicroscope at 16 - 24x.

Abomasal parasite counts

Caribou abomasa were collected fresh in the field shortly after animals were eviscerated by hunters. Both ends were tied off tightly using twine before the abomasum was excised and frozen. It was later thawed, opened and emptied into a shallow pan. The mucosal lining was gently scraped and the contents washed into a 4 L bottle which was topped up with 5% formalin, capped, labeled and stored until sub-sampled later and searched for nematodes. The fixed samples were poured gently through a No.100 mesh US standard sieve. The material remaining on the screen was back-flushed into a plastic container and topped up to a volume of 5 L with distilled water. After thorough mixing using a wide spatula, five 50 mL plastic centrifuge tubes, held together with an elastic around a piece of doweling, were immersed into the mixture, allowed to fill and then quickly removed. This procedure was repeated to produce a total of 10, 50 mL sub-samples. Each of these was allowed to settle for at least 15 minutes before being decanted and the sediment transferred, 2-3 mL at a time, into a gridded Petri dish and examined for worms using a stereoscope at 16x.

The entire wall of a sub-sample of abomasa was thawed and digested in artificial pepsin solution (30 g of pepsin concentration (1:3000), 33 mL of concentrated HCl per 5 L of distilled water) for 12 h at 37°C with stirring at 4 h intervals. The digesta was poured through a 1 mm mesh screen and then through a No.100 mesh US standard sieve. Material remaining on the sieve was back-flushed into a plastic container and topped up to 5 L. Sub-sampling and counting of worms was performed as described for the abomasal contents.

All worms longer than 1 mm were counted, removed and stored in 70% ethanol for identification. The mean number of worms in the 10, 50 mL sub-samples was multiplied by 100 to estimate the total number of worms present in each abomasum and to be able to compare to other studys. Thirty worms were randomly selected from each abomasum sample, cleared using lactophenol, and identified using a compound microscope and keys to the trichostrongyles by Durette-Desset (1983) and Fruetel and Lankester (1989). The proportion of different species was estimated by counting at least 800 males from a pooled sample of worms from all abomasa from a particular herd. Following Eve and Kellogg (1977), the abomasal parasite count (APC) used here in analyses represents the total number of all nematodes present in a sample, disregarding species differences.

Data were analyzed using the Statistical Package for the Social Sciences (SPSS), version 9.0 (SPSS Inc. Chicago, Illinois, USA). Non-parametric stastistical tests were used as I was unable to achieve homogeny of variance by data transformation. Comparisons of the mean larval intensity and abundance between years (1998/99 - 1999/00), seasons and locations were performed using the Kruskal Wallis one-way analysis of variance. Mann Whitney U tests were used to compare the same variables with regards to age and sex of caribou host. Chi Square analysis was used to detect differences in the prevalence of infection (%) and the frequency of migrating worms in the cranium between locations, ages and seasons. Spearman rank correlation tests were used to examine relationships between adult worms in the skeletal musculature and mean intensity of larvae produced; abundance of *E. rangiferi* in relation to herd density and climatic variables, and mean intensity of abomasal worms in relation to herd density and climate.

Results

Larval dimensions

The mean length of dorsal-spined nematode larvae passed in the feces of caribou varied in relation to herd, age of caribou and sampling time (Table 3). Overall, the mean length of larvae passed by caribou of the Cape Shore and Bay de Verde herds were significantly shorter than those from all other herds (U=2,899, P=0.355) and resembled larvae of the muscle worm, *P. andersoni*. These larvae never exceeded 400 μm in length and occurred only in small fecal pellets in all three sampling periods. Small pellets are thought to be from calves or yearlings while large pellets are from older animals (see below).

The remaining seven herds were considered to have mixed infections since two different sized larvae were being passed. The mean lengths of larvae in small pellets in September did not differ from the short ones in the Cape Shore and Bay de Verde herds indicating the presence of *P. andersoni*. However, significantly longer larvae occurred in the seven herds in December (H=8.13, P=0.04) and February (H=10, P=0.03) samples. The longer larvae reached 470 μm and resembled those of *E. rangiferi*. The mean length of larvae in large pellets was greater than those in small pellets in each sampling period (September: U=605, P<0.01; December: U=14,001, P<0.01 and February: U=28,264, P<0.01) but did not differ among the seven herds at any time.

Prevalence and intensity

Fecal samples from hunter-killed animals.

Feces from caribou killed by hunters were available in 2 periods, autumn (September and October) and winter (November and December) in each year of the study. In addition to parasitological data, they provided an opportunity to test for a possible relationship between the

Table 3. Mean length (μm) of dorsal-spined larvae from the feces of Newfoundland caribou.

	September			December			February		
Herd	Small[a]	Large	Total	Small	Large	Total	Small	Large	Total
St. Anthony	344±4[b] (290-400)	401±2 (376-430)	372±3 (290-430)	399±5 (350-462)	406±4 (370-446)	402±4 (350-446)	395±4 (320-440)	410±2 (380-430)	403±3 (320-430)
N. Peninsula	-	-	-	388±5 (346-432)	400±3 (370-430)	394±4 (346-430)	396±5 (368-416)	400±3 (376-420)	398±3 (368-420)
Gros Morne	-	-	-	384±5 (330-432)	402±3 (368-430)	393±4 (330-430)	402±5 (352-450)	413±4 (380-450)	408±4 (352-450)
Gaff Topsails	-	-	-	376±5 (332-442)	399±3 (370-445)	387±4 (332-445)	396±3 (370-432)	403±3 (378-430)	400±3 (370-430)
Middle Ridge	353±3 (316-390)	386±3 (354-422)	369±3 (316-422)	388±4 (340-430)	406±4 (380-426)	397±4 (340-426)	405±5 (360-466)	412±3 (388-446)	409±3 (360-446)
Merasheen	333±6 (288-380)	390±3 (360-422)	361±4 (288-422)	391±4 (340-444)	400±3 (370-460)	396±3 (340-460)	398±4 (372-422)	402±3 (370-426)	400±4 (372-426)
Avalon	343±4 (290-380)	395±4 (350-460)	369±4 (290-460)	386±5 (329-436)	413±5 (368-470)	400±5 (329-470)	406±6 (344-450)	421±4 (380-460)	414±4 (344-460)
Cape Shore	341±6 (290-376)	-	341±6 (290-376)	346±4 (290-370)	-	346±4 (290-370)	350±3 (330-376)	-	350±3 (330-376)
Bay de Verde	-	-	-	339±3 (312-370)	-	339±3 (312-370)	350±3 (310-375)	-	350±3 (310-375)

[a] Small = pellets with mean length ≤ 1.4 cm; Large = pellets with mean length >1.4 cm.

[b] Mean length of dorsal spined larvae ± S.E. subtended by range in brackets. Measurements of 30 larvae pooled from samples examined.

size of fecal pellets and caribou age. The mean length of pellets separated into three size groups, those produced by calves (4-7 months old, assuming 1 June birth), yearlings (16-19 months) and older animals (28 months and older) (Fig. 2). This relationship was used later as an estimate of the age of animals producing pellets that were collected directly off caribou range. Because of a limited number of calf pellets collected, analysis of larval abundance was done using only two different size classes (U=5,014, P=0.00). Small pellets with a mean length less than 1.4 cm were considered to be from calves or yearlings while longer ones, referred to as large pellets, were considered to be from animals 2 years and older.

In 166 fecal samples from caribou killed by hunters, the prevalence of dorsal-spined larvae ranged from a low of 24% in the Middle Ridge herd to 76% in the Avalon herd (Table 4). Overall, the mean intensity of larvae differed among herds (H=19, P=0.002) but only during the autumn period (H=14, P=0.02) with animals from Merasheen passing the most. Only the Avalon herd showed an increase in larval output from autumn to winter. (U=174, P=0.004).

Males on average passed more larvae than female caribou but the difference was not significant overall or within each season. Only male caribou passed more larvae in winter than in autumn (U=93, P=0.01). Mean intensity did not increase with age of caribou, overall or within seasons. Only yearling animals on the Avalon passed more larvae than other age classes in the same herd (U=7, P=0.03).

Ground-collected fecal samples

A total of 931 fecal samples were collected off caribou range during 3 sampling periods (September, December and February) and from hunter-killed animals in September and December (Table 5). Prevalence and mean intensity data did not differ between sampling years (1998-1999

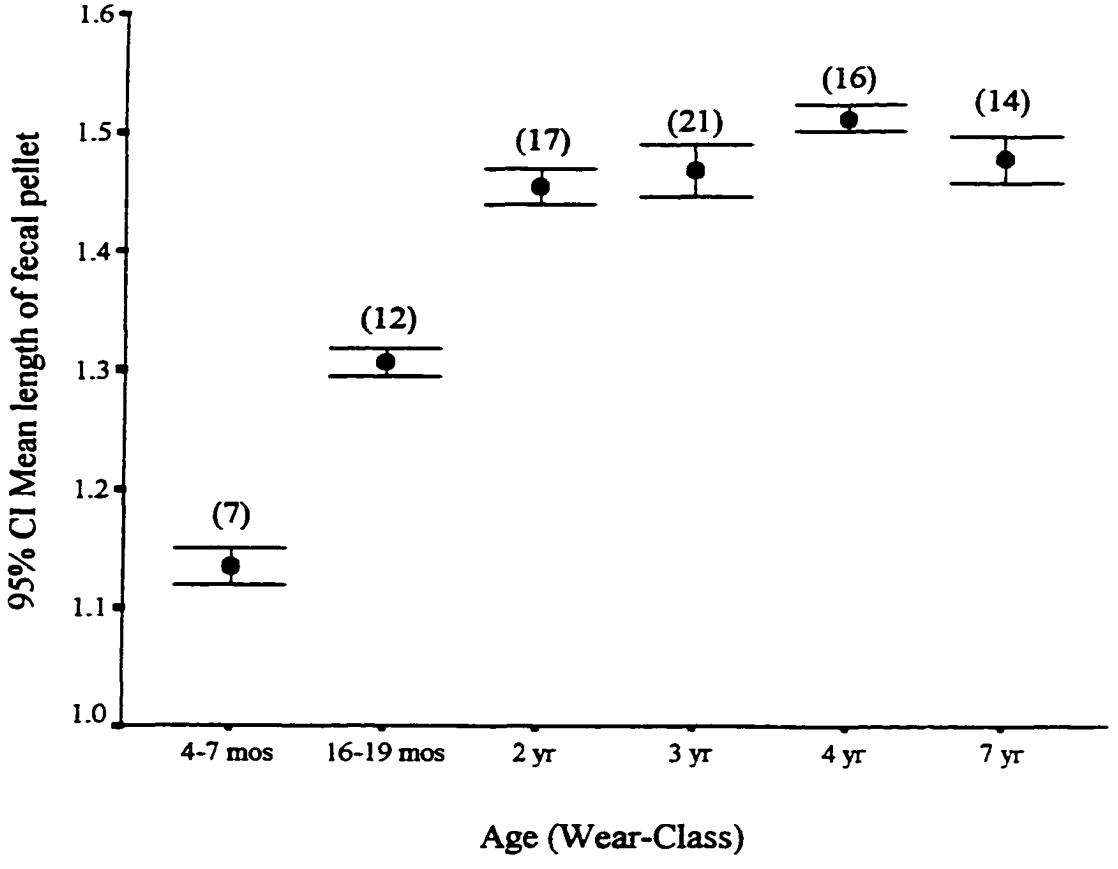


Fig 2. Relationship between mean maximum length of fecal pellets and age (tooth eruption and wear class) of caribou from Newfoundland.

Table 4. Mean intensity and prevalence of dorsal-spined larvae in feces of hunter-killed caribou from different herds in Newfoundland.

	Avalon		Cape Shore		Middle Ridge		Merasheen		St. Anthony	
Age by Season	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Autumn[a]										
0[b]	-	63±26[c] (100;2)	-	-	113 (100;1)	-	-	-	0 (0;1)	-
1	290±255 (86;7)	333±158 (83;6)	141 (50;2)	-	24 (33;3)	0 (0;2)	25±13 (67;6)	8 (50;2)	7 (100;1)	0 (0;2)
2+	191±166 (60;15)	30±6 (71;21)	0 (0;3)	-	60±46 (25;8)	0 (0;5)	817±801 (21;19)	27 (20;5)	10±3 (29;7)	3±0.3 (75;4)
Total	154±61 (72;51)		91±48 (20;5)		64±26 (16;19)		340±320 (31;32)		6±2 (40;15)	
Winter										
0	-	37±11 (100;2)	-	38±12 (100;4)	-	-		-	233 (100;1)	-
1	1281±464 (100;4)	288 (100;1)	82±43 (75;4)	0 (0;10)	-	16 (100;1)	-	-	1.3 (25;4)	-
2+	84±27 (75;4)	464±358 (80;10)	0 (0;7)	-	0 (0;1)	-	-	-	0 (0;5)	27±23 (100;4)
Total	525±208 (85;21)		68±24 (28;25)		16 (50;2)		-		57±38 (38;16)	
Sex totals	402±150 (73;30)	192±92 (79;42)	117±34 (15;26)	38±12 (28;14)	64±26 (31;13)	16 (13;8)	421±400 (32;25)	18±10 (28;7)	53±45 (26;19)	17±13 (58;12)
Overall	276±82 (76;52)		77±22 (28;30)		55±23 (24;21)		341±14 (31;32)		32±20 (39;31)	

[a] Autumn(September 6- October 31); Winter (November 1- December 31)

[b] Age classses: 0 = calves; 1 = yearlings; 2+ = 2-10 years of age

[c] Intensity values expressed as larvae/g of dried feces; mean ± S.E. subtended in brackets by prevalence; sample size.

Table 5. Mean intensity of dorsal-spined larvae in fecal pellets of caribou in Newfoundland (off ground and killed by hunters).

	September			December			February			
Herd	Small[a]	Large	Total	Small	Large	Total	Small	Large	Total	Overall
St. Anthony	13 ±6[b] (50)	0 (0)	13 ±6 (36)	156 ±43 (66)	59 ±13 (57)	105 ±23 (61)	679±175 (77)	159±48 (63)	449±107 (70)	277±58 (62)
N. Peninsula	-	-	-	77 ±17 (61)	73 ±16 (52)	71 ±13 (57)	587±332 (45)	88±39 (88)	213±96 (71)	241±98 (63)
Gros Morne	-	-	-	56±15 (59)	54 ±15 (63)	55 ±11 (63)	363±110 (56)	268±91 (81)	217±46 (69)	211±47 (66)
Gaff Topsails	-	-	-	63±29 (26)	512 (22)	138±79 (22)	998±939 (21)	454±148 (57)	514±161 (48)	446±134 (40)
Middle Ridge	106 (20)	24.5 (14)	63±50 (17)	63 ±21 (65)	58±21 (48)	61 ±16 (48)	319±91 (70)	140±37 (75)	217±46 (73)	116±33 (57)
Merasheen	11±3.6 (29)	550±534 (29)	549±535 (29)	301±85 (67)	158±48 (74)	204 ±44 (71)	531±210 (59)	217±61 (68)	319±82 (65)	286±64 (58)
Avalon	413±194 (79)	72±38 (71)	204±81 (74)	405±251 (90)	68 ±13 (87)	180±87 (87)	706±202 (89)	250±60 (91)	419±89 (90)	286±51 (83)
Cape Shore	196 ±7.1 (22)	0 (0)	196 (11)	625±216 (43)	0 (0)	625±216 (21)	1695±452 (44)	0 (0)	1695±452 (21)	936±190 (22)
Bay de Verde	-	-	-	375±136 (56)	0 (0)	375 ±136 (22)	2693±591 (53)	0 (0)	2693±591 (29)	2209±505 (27)

[a] Small = pellets with mean length ≤ 1.4 cm; Large = pellets with mean length >1.4 cm.

[b] Intensity values expressed as larvae/g of dried feces; mean ± S.E. subtended by prevalence in brackets. Sample sizes given in Table 7.

and 1999-2000) and therefore were pooled for all further analyses. Overall, prevalence was lowest in the Cape Shore and Bay de Verde herds (22% and 27%, respectively) where only *P. andersoni* occurred. Mean intensity was highest in these herds (H=56, P=0.00) and only young animals were passing larvae.

In the seven herds with mixed infections, prevalence of larvae in feces ranged from 40% in the Gaff Topsails to 83% in the Avalon herd. Mean intensity was greatest in the Gaff Topsails herd and lowest in the Middle Ridge and varied with season for all herds (H=56, P=0.00) except the Middle Ridge. Overall, the highest intensities occurred in both sizes of pellets in February. Mean intensity did not differ among herds when pellet size classes were considered separately for each season. Mean intensity was greater in small than in large pellets but only in the Avalon herd (September U=101, P=0.03; December U= 41, P=0.04; February U=139, P=0.01) and in the St. Anthony herd in February (U=115, P=0.01). The Gaff Topsails herd had a greater intensity of larvae in the large pellets but only in December.

Avalon herd fecal samples

The Avalon herd was the most accessible making it possible to collect fecal samples off the ground every few months from September 1998 to April 2000. The prevalence of dorsal-spined larvae was high in both small and large pellets throughout most of the year (80-100 %) but declined somewhat during late summer (48-69 %) (Table 6; Fig. 3). Mean intensity did not vary between the two years but varied with month of sampling (H=57, P<0.001) for all pellets and for both small (H=24, P=0.01) and large (H=43, P<0.001) pellets. Small pellets had higher numbers of larvae than large pellets

Table 6. Mean intensity of dorsal-spined larvae in feces of caribou from the Avalon herd (September 1998 - April 2000).

Month 98-99	Small[a]	Large	Total	Month 99-00	Small	Large	Total
September '98	265 ±216[b] (7/9)	17 ± 5 (7/14)	141 ± 109 (19/23)	July '99	70 ± 50 (4/10)	91 ± 55 (5/15)	84 ± 39 (12/25)
December '98	483 ± 380 (6/6)	79 ± 15 (12/14)	214 ± 128 (18/20)	August '99	63 ± 33 (3/7)	24 ± 7 14/18	33 ± 9 (17/25)
February '99	956 ± 336 (13/14)	332 ± 103 (5/6)	610 ± 172 (18/20)	September '99	683 ± 304 (8/10)	30 ± 9 (17/19)	239 ± 112 (20/29)
April '99	1138 ± 466 (12/12)	111 ± 19 (24/25)	453 ± 172 (36/37)	December '99	225±77 (4/5)	22±6 (5/6)	112±47 (9/11)
May '99	2186 ±1036 (5/5)	118 ± 44 (8/8)	914 ± 472 (13/13)	February '00	484 ± 332 (15/15)	206 ± 74 (14/16)	296 ± 90 (29/31)
June '99	227 ± 133 (9/10)	45 ± 10 (11/12)	150 ± 64 (20/22)	April '00	515 ± 110 (9/9)	141 ± 59 (5/9)	381 ± 87 (14/18)

[a] Small = pellets with mean length ≤ 1.4 cm; Large = pellets with mean length >1.4 cm.

[b] Mean ± S.E. of larvae/g of dried feces subtended in brackets by number of positive samples/number examined.

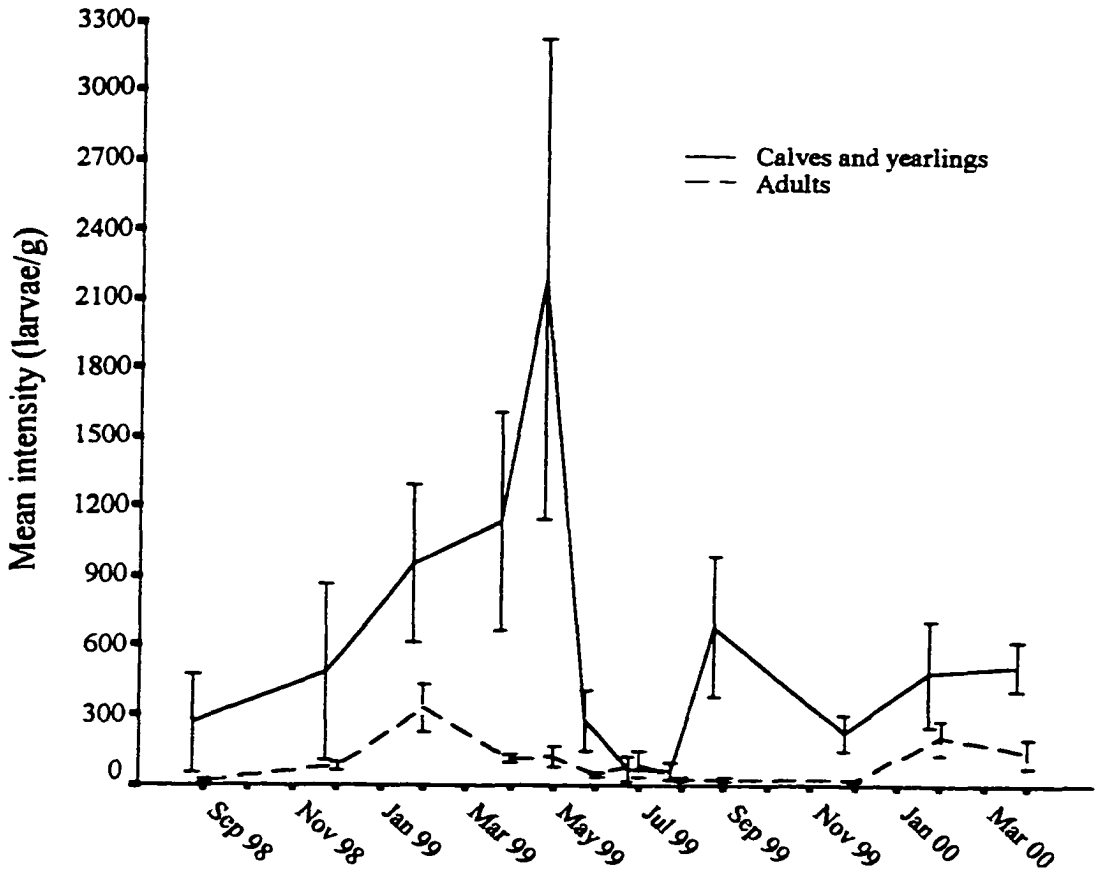


Fig 3. Monthly mean intensity of dorsal-spined larvae in the feces of caribou from the Avalon herd, Newfoundland

throughout the year. Larval numbers peaked in large pellets in February but not until April-May in small pellets. They declined in both pellet sizes over summer. In autumn, larval numbers in small pellets increased earlier and reached higher numbers than larvae in large pellets. The unusually high mean intensity for May 1999 may be somewhat distorted by two animals passing 3,012 and 5,693 larvae/g.

Abundance by season, age, climate and density among different herds

Factors affecting abundance of larvae (prevalence x mean intensity) were examined only in the seven herds with mixed infections (*E. rangiferi* and *P. andersoni*). Overall, there was a significant increase in larval abundance from September to February in both small ($H=9$, $P<0.01$) and large ($H=37$, $P<0.001$) pellets (Table 7). Larval abundance in small pellets varied among herds in all three sampling periods (September $H=10$, $P=0.02$; December $H=18$, $P=0.003$; February $H=19$, 0.01) and in large pellets in September ($H=17$, $P=0.001$) and December ($H=15$, $P=0.01$) but not in February.

A Spearman rank correlation analysis of larval abundance and various weather parameters used only larval counts from small feces in February and mean annual weather data for 1997 and 1998. These two years spanned the period in which the young cohort of caribou examined here became infected. Only February data were used since most worms acquired the previous year would be mature and passing larvae by this time. Larval abundance was positively correlated with mean annual minimum temperature ($r_s= 0.829$, $df=6$, $P=0.04$) and the number of days with maximum temperatures above 0°C ($r_s= 0.812$, $df=6$, $P=0.05$) and negatively correlated with mean summer temperatures ($r_s= - 0.830$, $df=6$, $P=0.04$). There was no significant correlation between parasite abundance and herd density ($r_s= - 0.143$, $df=6$, $P=0.79$).

Table 7. Abundance of dorsal-spined larvae in fecal pellets of caribou in Newfoundland.

	September			December			February			
Herd	Small[a]	Large	Total	Small	Large	Total	Small	Large	Total	Overall
St. Anthony	7±5[b] (4/8)	0 (0/7)	3±2 (4/15)	102±31 (19/29)	33±9 (21/37)	64±15 (40/66)	526±145 (24/31)	101±33 (19/30)	317±80 (43/61)	170±37 (87/142)
N. Peninsula	-	-	-	43±23 (11/18)	38±15 (10/19)	41±7 (21/37)	267±169 (5/11)	78±35 (15/17)	152±70 (20/28)	152±71 (41/65)
Gros Morne	-	-	-	33±11 (10/17)	36±18 (12/18)	35±8 (22/35)	204±72 (13/23)	216±76 (25/31)	211±53 (37/54)	142±33 (59/89)
Gaff Topsails	-	-	-	17±10 (5/19)	64±64 (1/8)	31±20 (6/27)	220±205 (3/14)	225±91 (24/42)	224±84 (27/56)	165±54 (33/83)
Middle Ridge	21±21 (1/5)	4±4 (1/7)	11±9 (2/12)	41±16 (11/17)	18±9 (5/16)	30±9 (16/33)	222±70 (16/23)	104±30 (21/28)	158±36 (37/51)	95±20 (55/96)
Merasheen	3±2 (2/7)	157±153 (6/21)	119±115 (8/28)	201±70 (8/12)	117±38 (17/23)	145±35 (25/35)	312±137 (10/17)	147±45 (21/31)	205±57 (31/48)	164±39 (64/111)
Avalon	327±157 (15/19)	51±27 (24/33)	152±61 (39/52)	364±228 (9/10)	58±12 (18/21)	157±76 (27/31)	632±14 (17/19)	227±56 (29/32)	378±82 (46/51)	237±44 (112/135)
Cape Shore	43±29 (2/9)	0 (0/9)	21±73 (2/18)	271±113 (10/23)	0 (0/24)	135±58 (10/47)	686±200 (12/27)	0 (0/30)	325±104 (12/57)	207±54 (27/122)
Bay de Verde	-	-	-	208±97 (5/9)	0 (0/13)	85±45 (5/22)	1421±383 (19/36)	0 (0/30)	775±225 (19/66)	602±172 (24/88)

[a]Small = pellets with mean length ≤ 1.4 cm; Large = pellets with mean length >1.4 cm.
[b]Values given are mean ± S.E. subtended in brackets by number infected/sample size.

Recent infections by age

Finding immature *E. rangiferi* migrating on the surface of the brain indicates that the caribou has been infected within the past 90 days. Such worms were present on the brains of 38% of 45 calves and yearlings examined from 5 herds with mixed infections (Table 8). However, worms were not found on the brain of any of 73 adult caribou from 4 of these herds. A notable exception was the Avalon herd in which 6 of 33 adults (up to 7 years old) had worms on the brain. The mean number of worms in the cranium was greater in calves and yearlings (6 ± 0.98, range 3-12) than in adult caribou (1.5 ± 0.34, range 1-3)(U= 3.5, P=0.01). No worms were found within the cranium of 39 caribou examined from the Cape Shore herd where only *P. andersoni* occurs.

Adult *E. rangiferi* vs. first-stage larvae in feces

The total number of adult *E. rangiferi* in the musculature and heads of infected caribou was correlated with the mean intensity of larvae passed in the feces (r_s=0.976, n=8) (Table 9; Fig. 4).

Microclimate

Data obtained from remote temperature recorders placed 2 cm above the surface on range occupied by 4 of the caribou herds generally showed a north-south gradient of warming mean annual temperatures (Table 10; Fig. 5). In the winter of 1999-2000, monthly mean temperatures from the Avalon did not drop below 0°C at any time. In contrast, temperatures from St. Anthony were below 0°C for the duration of winter (November -April). Data obtained from recorders placed on the Avalon range near Trepassey, showed that average temperatures 2 cm below the

Table 8. Prevalence (%) of *E. rangiferi* on the brains of hunter-killed caribou from different herds in Newfoundland.

Age	Avalon	Cape Shore	Middle Ridge	Merasheen	St. Anthony	Gaff Topsails	Totals
0[a]	83 (5/6)[b]	0 (0/4)	50 (1/2)	0 (0/2)	40 (2/5)	100 (1/1)	47 (9/19)
1	18 (4/13)	0 (0/5)	0 (0/3)	20 (1/5)	75 (3/4)	0 (0/5)	23 (8/35)
2+	18 (6/33)	0 (0/30)	0 (0/19)	0 (0/19)	0 (0/23)	0 (0/12)	4 (6/136)
Totals	29 (15/52)	0 (0/39)	4 (1/24)	4 (1/26)	16 (5/32)	5 (1/19)	12 (23/190)

[a]Age classes: 0=calves; 1=yearlings; 2+=2-10 years.

[b]Animals infected/examined; most had 1-2 worms but 5 calves (3 from the Avalon and 2 from St.Anthony) each had 12.

Table 9. Intensity of adult *E. rangiferi* and dorsal-spined larvae from caribou of known age and sex.

Area collected	Date of collection	Sex	Approx. age (months)	# of adult worms in muscle	Larvae/g of dried feces
Gaff Topsails*	5 Feb 84	f	9	6	29
Gaff Topsails*	28 Jan 84	f	9	5	6
Gaff Topsails*	21 March 84	f	10	14	121
Gaff Topsails*	20 March 84	f	10	18	41
St. Anthony	14 Dec 98	m	19	21	310
Avalon	20 Nov 98	m	19	83	2,090
Avalon	6 Jan 99	f	20	46	1,298

* Fong (1984).

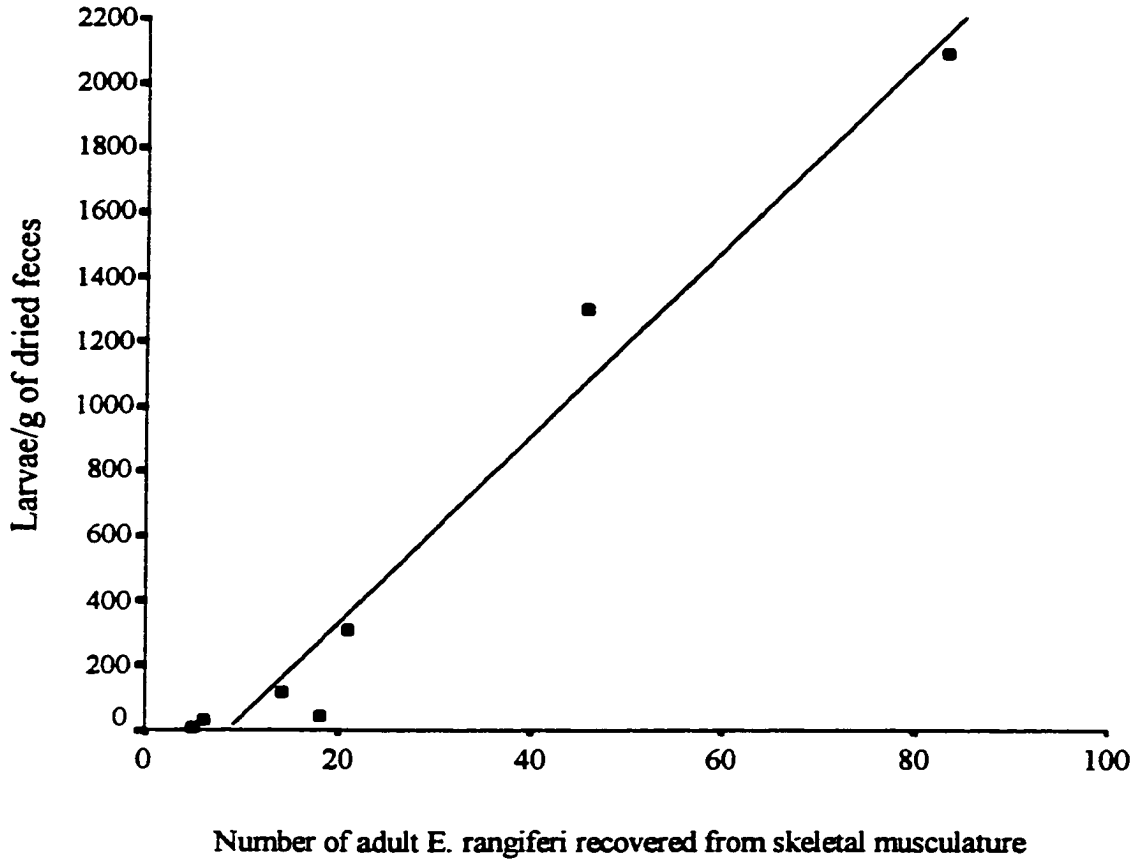


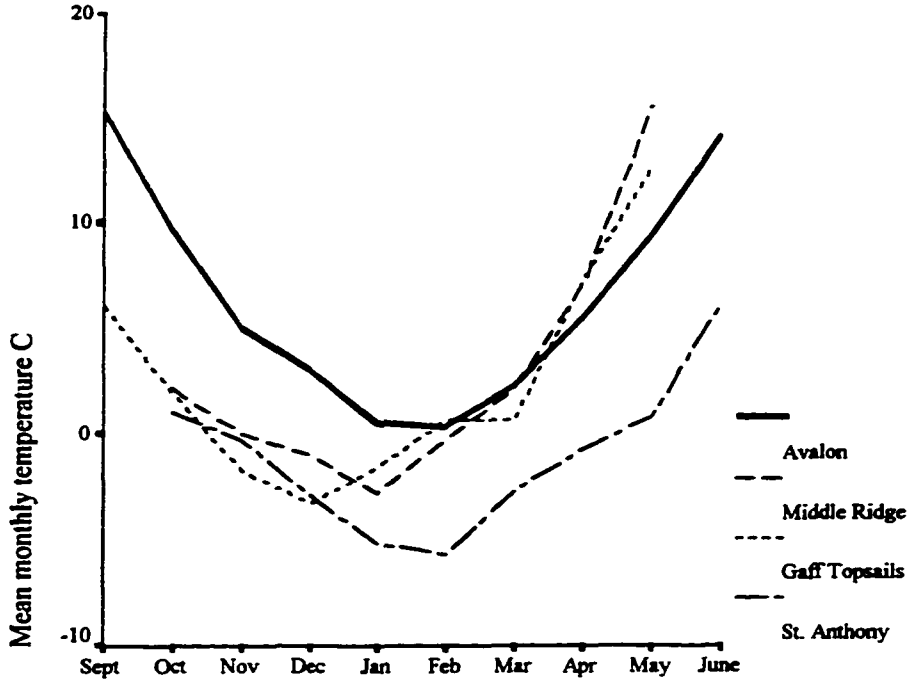
Fig 4. Relationship between the numbers of adult *E. rangiferi* in the skeletal musculature and intensity of dorsal-spined larvae in the feces of caribou from Newfoundland (r_s=0.976, $p<0.001$)

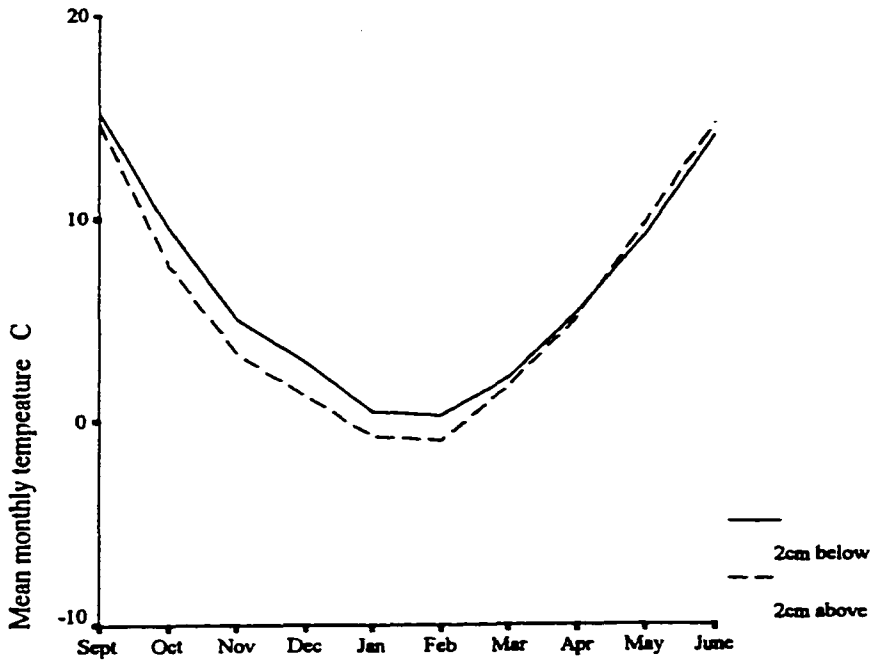
Table 10. Ground surface and below ground temperatures (°C) from areas occupied by 4 caribou herds in Newfoundland (1999-2000).

Area	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	June
St. Anthony[a]	-	1.0[b] (-0.6 - 6.6)	-0.3 (-1.5 - 6.2)	-2.9 (-10 - -1.1)	-5.2 (-14.1 - -1.1)	-5.7 (-13.5 - -1.1)	-2.7 (-7.9 - -1.1)	-0.8 (-1.5 - 2.0)	0.8 (-1.1 - 6.6)	6.1 (0.3 - 14.5)
Gaff Topsails	6.1 (0.3 - 13.0)	1.9 (-1.5 - 9.0)	-1.7 (-6.8 - 0.7)	-3.3 (-8.4 - -0.2)	-1.6 (-7.9 - 0.7)	0.6 (-2.0 - 1.2)	0.6 (-2.4 -3.3)	7.2 (-0.2 -13.7)	12.6 (6.2 - 18.0)	-
Middle Ridge	-	2.1 (-3.0 - 11.0)	0 (-3.9 - 6.2)	-1.0 (-4.3 - -0.2)	-2.8 (-8.4 - -0.2)	-0.3 (-3.4 - 4.6)	2.1 (-1.1 - 12.6)	7.0 (0.7 - 21.3)	15.5 (4.2 - 26.7)	-
Avalon (above)	14.7 (4.2 - 24.0)	7.7 (-2.9 - 18.7)	3.3 (-2.4 - 9.8)	1.3 (-4.3 - 9.8)	-0.7 (-6.3 - 6.6)	-0.9 (-4.3 - 3.7)	1.8 (-5.3 - 17.9)	5.2 (-3.4 - 23.2)	9.9 (-3.4 - 34.0)	14.7 (0.3 - 32.8)
Avalon (below)	15.3 (9.0 - 19.8)	9.6 (2.5 - 15.2)	5.0 (1.6 - 8.6)	3.0 (0.3 - 7.4)	0.5 (-1.1 - 3.7)	0.3 (-0.6 - 2.5)	2.2 (0.3 - 10.2)	5.4 (1.6 - 11.4)	9.3 (3.3 - 17.9)	14.1 (7.0 - 31.0)

[a]Data from temperature recorders placed at the surface covered by vegetation; on the Avalon near Trepassey, a recorder was also placed 2 cm below surface.

[b]Mean monthly temperatures subtended in brackets by range.





surface were 0.8°C warmer than surface air temperatures. These differences occurred in the cooler autumn and winter months (September-March) in the absence of snow ground cover.

Abomasal nematodes

Ostertagia gruhneri occurred in 100% of caribou of all herds studied and was the dominant abomasal nematode found. Its relative numbers ranged from 76 to 99% of the mean abomasal parasite counts (APCs) from the Cape Shore and Middle Ridge herds, respectively (Table 11). *Trichostrongylus axei* was also present in all herds but in lower numbers representing a range of 12 and 23% of the APCs for Merasheen and Cape Shore, respectively, and 5% or less for the remaining herds. A few *Haemonchus contortus* were infrequently found in the Cape Shore and St. Anthony animals.

Mean abomasal parasite counts ranged from a low of 2,513 in St. Anthony to 12,245 in the Cape Shore caribou (Table 11). The APCs in St. Anthony animals were significantly lower than all other herds ($H=36$, $P<0.000$) but no difference existed between the two most heavily infected herds, the Cape Shore and Avalon. The APCs did not vary between the sexes but were lower in calves (2,393 ± 940, n=3) than in older age classes (8,613 ± 880, n=67), that did not differ from each other. Digestion of the entire wall of the abomasa released additional worms (up to 2.5 mm long) but their relative numbers never exceeded 2.5 % of the APCs and data were not, therefore, included in analyses. Spearman rank correlation analysis (excluding calves) showed a positive correlation between mean APCs and the number of days when the mean daily temperature was greater than 0 °C ($r_s=1.0$,$df=4$, $P\leq 0.01$), the annual mean temperature ($r_s=1.0$,

Table 11. Abomasal parasite counts (APC) from caribou herds in Newfoundland.

Herd	APC	No. of abomasa	% of worms in mucosa	% *O. gruhneri*	% *T. axei*	% *H. contortus*	Estimated caribou density[d]
St. Anthony	2,513± 281[a]	18	1.3	98[b] (100)[c]	1 (11)	1 (11)	2.0
Middle Ridge	4,929 ± 837	11	2.0	99 (100)	1 (27)	0 (0)	3.0
Merasheen	6,640 ± 1,436	11	2.0	88 (100)	12 (45)	0 (0)	2.6
Cape Shore	12,245 ± 2,470	17	2.2	76 (100)	23 (76)	1 (6)	2.4
Avalon	10,395 ± 1,046	28	1.9	95[b] (100)[c]	5 (43)	0 (0)	0.5

[a]Mean ± S.E.
[b]Percentages based on identifying sub-samples of at least 800 adult male worms.
[c]Prevalence of infection.
[d]Animals /km^2

df=4, P≤0.01), total annual rainfall (r_s=1.0, df=4, P≤0.01) and total annual precipitation (r_s=1.0, df=4, P≤0.01). Mean abomasal worm counts were negatively correlated with total annual snowfall (r_s= - 1.0, df=4, P≤0.01). There was no significant relationship between herd density and APCs (r_s = - 0.400, df=4, P=0.600).

Discussion

Concomitant infections of *E. rangiferi* and *P. andersoni* were found in seven of the nine Newfoundland caribou herds studied. Animals in the Cape Shore and Bay de Verde herds had only *P. andersoni.* This parasite is known to occur widely in woodland and barrenground caribou across North America (Lankester and Hauta 1989), whereas, Newfoundland is the only place in North America where *E. rangiferi* has been found. Since its introduction in 1908, *E. rangiferi* took about 80 years to spread from St. Anthony at the northern tip of Newfoundland where Norwegian reindeer were first landed, to the Avalon Peninsula in the extreme south. A barrier that probably slowed its spread onto the Avalon Peninsula was the narrow isthmus of land at Come By Chance. Based on past examinations of animals and fecal samples, Lankester and Fong (1998) suggested that *E. rangiferi* did not reach the Avalon herd until about 1990. Historical records presented here strengthen this conclusion. Caribou used to establish the Cape Shore and Bay de Verde herds were only translocated recently from the Avalon herd in 1977 and 1989, respectively, and neither have *E. rangiferi.* The Cape Shore herd is probably at greatest risk of future infection because of its closer proximity to the Avalon herd.

Parasite identifications were based on the morphometrics of adult male worms from caribou as well as dimensions of first-stage larvae recovered from feces. From published reports, the mean length of *P. andersoni* larvae (358±16 μm, range 319-385 μm) (Prestwood 1972, Lankester and Hauta 1989) is shorter than that of *E. rangiferi* (421±13 μm, 370- 445 μm) (Lorenzen 1979)). In this study, larvae from caribou of the Cape Shore and Bay de Verde herds with only *P. andersoni* were 290-370 μm long while those from herds with both *P. andersoni* and *E. rangiferi* were 288-470μm. The mean lengths of larvae passed by caribou with concomitant

infections will vary with respect to the relative numbers of larvae being produced by each of the two species present.

The size of fecal pellets collected directly off caribou range was used to estimate the age of the animals that produced them and was a convenient way of increasing age-specific sample sizes. The relationship was established using pellets from known-aged animals killed by hunters from September to December. Hence, small pellets (≤ 1.4 cm long) collected directly off range in September and December were considered to have been deposited by young animals including calves when they were 4 and 7 months old and yearlings 16 and 19 months old, respectively. Likewise, small pellets collected off range in February were from 9 month old calves and probably from 21 month old yearlings as well. MacCracken and Ballenberghe (1987) examined the use of pellet dimensions for ageing moose (*Alces alces*). They chose to use pellet volume, rather than length, because it provided an estimate of relative age (either yearling or adult) as well as sex of moose. The ability to distinguish pellets of young and old animals is particularly useful in parasitological studies since the production of larvae or eggs often differs markedly between these two host age groups.

The discovery of two herds infected with only *P. andersoni* provided an opportunity to obtain specific data on its larval output in relation to season and host age. Mean intensity peaked in February at up to 2,693 larvae/g of dried feces but larvae occurred only in small pellets from young animals. This was consistent with the findings of Lankester and Fong (1998) who recovered adult and larval *P. andersoni* from 7-13 month old caribou of the Middle Ridge herd but not from 19 month old animals or adults. In barrenground caribou of the Beverly herd, central Northwest Territories, Lankester and Hauta (1989) found a much lower mean intensity of

P. andersoni larvae (13 larvae/g of fresh feces) but calves and yearlings similarly passed the most larvae and in spring (March and early April). Infections in the Beverly herd differed in that small numbers continued to be produced by older animals although this may have been a function of a later sampling time (March-April vs February).

Monthly sampling of the Avalon herd provided the opportunity to understand changes in larval output by animals with mixed infections in relation to season and host age. Larval output by young animals peaked in September and then again in February through to May. Output by adult animals peaked each February. The two peaks seen in young animals coincided with the known development of *P. andersoni* and *E. rangiferi*. As the smaller pellet class contained several new calves, the peak in larval numbers in September was probably due to *P. andersoni*. Larvae of this species appear in feces as early as 51 days after infection in white-tails and within 66 days in caribou but numbers decline rapidly thereafter in both hosts (Nettles and Prestwood 1976; Pybus and Samuel 1981,1984; Lankester and Hauta 1989). The second peak seen from February to May was due mostly to *E. rangiferi* that requires 4-4.5 months to become patent (Handeland et al. 1994). This was confirmed by finding shorter larvae in young animals in September ($\bar{x}$ =343±4; range 290-380) than in February ($\bar{x}$=406±6; 344-450). The larval peak in older caribou seen each February probably represents the "spring rise" which occurs in many related nematodes (Prosl and Kutzer 1980; Samuel et al. 1985; Demiaszkiewicz 1989; Lankester and Hauta 1989; Slomke et al. 1995) and is presumed to maximize larval output in spring when conditions are optimal for infection of gastropods.

Of the 7 caribou herds with mixed infections, calves and yearlings passed twice as many larvae as older caribou. A similar pattern of higher larval output by young naive animals is seen in

other cervids with elaphostrongylin nematodes including white-tailed deer with *P. tenuis* (Anderson 1963; Slomke et al. 1995) or *P. andersoni* (Nettles and Prestwood 1976) and mule deer with *P. odocoilei* (Samuel et al. 1985). Adult male and female caribou shed similar numbers of larvae both in autumn (September-October) and winter (November-December). This contrasts with a report by Halverson et al. (1985) who found an increase in larval output by male reindeer in autumn corresponding with the rut and by females in the spring prior to calving. These increases in larval production were inversely related to titres of larval-specific antibody believed to fluctuate in relation to stress during these periods (Gaudernack et al. 1984).

By February, young animals with concomitant infections of *P. andersoni* and *E. rangiferi* were producing only half as many larvae as animals with *P. andersoni* alone and the greater mean length of the larvae suggested that most were *E. rangiferi*. Experimental studies indicate that larval production by *P. andersoni* in caribou and white-tailed deer rises quickly after patency to peak in 2-8 weeks and then declines (Lankester and Hauta 1989; Nettles and Prestwood 1976; Pybus and Samuel 1981). Clearly, larval production by *P. andersoni* dropped off more quickly in mixed infections than when alone. A similar interaction between *P. andersoni* and *P. tenuis* in white-tailed deer was noted by Lankester and Hauta (1989) who commented on the rarity of dual infections and suggested that the lack of geographic overlap between the two parasites in the southeastern coastal plain States may result from a form of cross-immunity that prevents sympatry. In Newfoundland, *P. andersoni* has not been excluded by the presence of *E. rangiferi* but its larval output in individuals with concomitant infections appears greatly reduced.

Despite the confounding aspects of concomitant infections, I conclude that counts of dorsal-spined larvae in small pellets (calves and yearlings) in February can provide a reasonable

approximation of the level of *E. rangiferi* infection in animals and that this measure can be used to evaluate factors affecting transmission of the parasite. This is corroborated by the observation that the numbers of dorsal-spined larvae passed in caribou feces was correlated with the number of adult *E. rangiferi* present in the musculature of young animals. Although much of the strength of this correlation was derived from animals necropsied at 19-21 months of age, this is the age of yearling animals at the time of the February fecal collections. By this time, as well, *P. andersoni* larval production in concomitant infections has stopped and only *E. rangiferi* larvae are being passed. Some small pellets collected at this time will have come from 9 month old calves and the numbers of *P. andersoni* larvae are much reduced in their feces by February. Pybus and Samuel (1984) similarly found a positive relationship between numbers of larvae shed and adult *P. andersoni* in mule deer and white-tailed deer. However, neither Bogacyzk (1990) nor Slomke et al. (1995) found evidence of such a relationship for *P. tenuis* in white-tailed deer, but both used infected animals of all ages. In the present study, older animals were excluded from the correlation analysis, since several age-related factors such as increased immune response to eggs or larvae, or decreased fecundity of older worms may mask any relationship with larval output (Slomke et al. 1995). As well, caribou normally do not acquire additional worms after about their second summer of life. Evidence for this was the lack of migrating worms in the cranium of older animals (except in the Avalon herd) . For these reasons, the causes of any year to year changes in transmission can only be identified by monitoring levels of larval output in the calf and yearling cohorts.

Mean abundance of a parasite, in the sense of Bush et al. (1997), was considered to provide the best measure of the level of infection in the different herds. Denoted as the product of

prevalence x mean intensity of larvae in small feces in February, it is here considered to reflect the average number of adult *E. rangiferi* acquired by calves and yearlings over the previous 2 summers. The mean abundance is also a reasonable measure of the numbers of larvae being shed onto caribou range and contributing to future infections. The mean abundance of *E. rangiferi* was positively correlated with the number of days with maximum temperatures above 0°C and varied from lows of 259 and 262 days in the vicinity of the Gros Morne and Northern Peninsula herds to 305 days in the area occupied by the Avalon herd. Mean abundance was also correlated with mean annual minimum air temperatures but not with mean annual temperatures. As well, the mean abundance of *E. rangiferi* was significantly lower in herds experiencing mean summer temperatures above 13°C than in herds at cooler temperatures. These results allude to the importance of moderate temperatures in maximizing abundance.

Temperature may have its greatest affect on parasite abundance by influencing gastropod movement on vegetation and the likelihood of them being accidentally eaten by caribou. The principal host of *E. rangiferi* in Newfoundland is known to be *Deroceras laeve* (Lankester and Fong 1998). This small dark slug is extremely abundant over most of the island. It moves relatively quickly and can be found well up on ground vegetation during cool wet periods. It remains active at temperatures approaching freezing and is one of the first species active in the spring and one of the last seen in autumn (Lankester and Peterson 1996). Warming, dry or windy conditions drive this slug below the surface vegetation reducing its availability to caribou. The number of days with temperatures above 0°C is, therefore, a measure of the period in which *D. laeve* is active and hence approximates the length of the annual transmission period for *E. rangiferi*. Peterson et al. (1996) similarly found a correlation between prevalence of *P. tenuis* in

white-tailed deer and the length of time in the fall of the year when conditions still allowed the accidental ingestion of gastropods, including *D. laeve.*

In Newfoundland, the number of days with mean temperatures above 13°C likely reflects the amount of weather with warmer, drying conditions which are unsuitable for slug movement on vegetation and indicate a shortened transmission period. Little is known of the ability of first-stage *E. rangiferi* larvae to survive higher field temperatures but most elaphostrongylin larvae are on the surface of fecal pellets and can be easily washed off by rain into the soil where survival is probably higher (Lankester 2000). A more likely result of higher temperatures, along with drying conditions, may be to reduce the mobility of slugs on vegetation and their availability to caribou.

Temperature is also known to affect the rate of development and survival of *E. rangiferi* larvae in gastropods. Almost no development of *E. rangiferi* occurs at temperatures below 10°C (Halvorsen and Skorping 1982, Bodnar 1998). Survival of second-stage larvae may be diminished at lower temperatures (Schjetlin and Skorping 1995) but infective larvae certainly survive in gastropods over winter (Skorping and Andersen 1991). The rate of larval development increases exponentially above 10°C and varies with gastropod host species. For example, development to the infective stage in *Arianta arbustorum* takes 75 days at 12°C but only 11 days at 28°C (Halverson and Skorping 1982). In *D. laeve* held at 14°C, 17% of *E. rangiferi* larvae had reached the infective stage by 6 wks and all were in the infective stage by 10 weeks (Bodnar 1998). In the present study, the mean number of days above 10°C varied from a low of 117 days in the north at St. Anthony and 155 days (32 % more) in the area occupied by the Avalon herd in the south. However, no correlation was observed between the abundance of *E. rangiferi* in the different herds and the number of days above 10°C suggesting that the abundance of this parasite in

different regions of Newfoundland is not limited by temperatures required for the timely development of larvae to the infective stage.

I found no correlation between herd density and the abundance of *E. rangiferi* in the 7 herds with mixed infections. As well, the relationship between the abundance of *P. andersoni* and herd density was the opposite of what one might expect. The Cape Shore herd with an estimated density of 2.4 caribou per km^2 had about half the abundance of *P. andersoni* larvae (686 ± 200) as the Bay de Verde herd (1421 ± 383) with an estimated density of 0.1/km^2. Despite the intuitive expectation that parasite transmission rates will increase with increased host density, such a relationship is often difficult to demonstrate. Data used to test such hypotheses are frequently weakened by the low accuracy of host density estimates. This is particularly true for gregarious caribou that segregate seasonally by sex , and whose habitat use patterns change over longer time frames (Thomas 1996). Other studies of protostrongylids have also failed to detect a clear relationship between host density and parasite numbers. For example, the mean intensity of adult *P. tenuis* changes little with changes in white-tailed deer density (Gilbert 1973, Bogacyzk et al. 1993; Slomke et al. 1995). In fact, an immunologically determined threshold number of adult worms may be reached, after which deer do not acquire additional worms (Slomke et al. 1995). Deer at markedly different densities (2 animals/km^2 and 30 animals/km^2) had similar numbers of adult *P. tenuis.* But for reasons that could not be explained, the deer at the higher density were passing significantly more larvae. Peterson et al. (1996) did find that the prevalence *P. tenuis* larvae in feces was correlated with deer density but numbers of adults were not examined. The lack of an apparent relationship between abundance of *E. rangiferi* and caribou density possibly is due in part to similar, poorly understood processes.

A better understanding of the factors that determine abundance might be gained by examining what causes epizootics of CSE. The severity of elaphostrongylosis is dose dependant (Halvorsen 1986b) and animals showing signs of CSE, the most severe form of the disease, are believed to have ingested the most infective larvae. Higher rates of CSE are probably an indication, therefore, of an increased abundance of the parasite and would be expected in those areas or in those years with conditions favouring high transmission and abundance. Our observations support this hypothesis. During the present study, the only reported cases of CSE were in the Avalon and St. Anthony herds (Con Finlay and Mark Lawlor pers. comm.), the two herds with the highest abundance of larvae in feces of young animals in February.

Higher than average temperatures have been associated with epizootics of CSE in calf reindeer and small ruminants in northern Norway (Halverson et al 1980, Handeland and Slettbakk 1994, 1995). The explanation for the apparent relationship between outbreaks of late winter CSE and warmer than usual conditions the previous summer has been based on laboratory studies of larval development and survival in gastropods (Halverson et al 1980, Halvorsen 1986a). Development is positively correlated with increasing temperatures. However, at temperatures below 10°C, development stopped and survival of second and third-stage larvae was reduced. Therefore, during normally short, cool summers in northern Norway, the number of larvae reaching the infective third-stage before winter would be limited. Those still in the second-stage, as well as thirds, would experience some mortality over winter and be available in lowered numbers when gastropods were again active in spring. On the other hand, higher than usual summer temperatures, they argued, would result in more larvae reaching the infective stage over the relatively short summers and more being available to calves before the onset of winter. This

seems a plausible explanation for epizootics in Northern Norway which is at about 70° N. However, In Newfoundland at about 49°N, the length of the season suitable for transmission, rather than unusually high temperatures, seems to be most important in determining abundance of *E. rangiferi* and may in fact be the better predictor of the likelihood of epizootics of CSE.

Historically, there has been only one confirmed epizootic of CSE in caribou of Newfoundland (Lankester and Fong 1989). This occurred in the Gaff Topsails herd from 1981-1985. Sick animals appeared tame, stood alone for long periods with the head held low and the back arched. Some showed marked weakness of the hind quarters, dragging one or both back legs. Of 17 animals submitted for necropsy, all had *E. rangiferi,* all were observed from January to April, all but 1 were calves and 12 of 15 sexed animals were males. Records do not indicate any perceptible decline in the Gaff Topsails herd as a result of the epizootic. Reports of CSE in Fenoscandinavia similarly are seen in late winter and involve primarily male calves (Mitskevich 1929; Roneus and Nordkvist 1962; Halvorsen 1986b). Males are more likely than females to exhibit CSE because they eat more and ingest the most larvae (Halvorsen 1986b). Climate data for the Gaff Topsails area over the 5 years of the epizootic showed significantly higher mean annual temperatures ($\bar{x}$=4.1±0.5°C; U=4,P=0.03) and significantly lower total annual snowfall ($\bar{x}$=167±11cm; U=0,P=0.003) than means for the following 11 years (1987-1997)($\bar{x}$=2.8±0.2°C and $\bar{x}$=387±21 cm), when no unusually high numbers of animals with CSE were seen. Longer periods for parasite transmission could, therefore, have been responsible for this epizootic spanning about 5 years.

An earlier study by Bergerud (1971) recorded unusually high calf mortality in the Interior herd of Newfoundland (probably the Middle Ridge herd) from 1959-1962. Male calf mortality was

higher than females. Calves were reported as being in poor condition, commonly seen separated from the rest of the herd and showing signs of pneumonia. This description of sick caribou resembles clinical CSE. However, many calves appeared to have died of bacterial septicemia and puncture wounds made by lynx (*Lynx canadensis*). The mean annual rate of population increase for this Interior herd was estimated at 3.3% from 1961-1967 whereas the Avalon herd over the same period was growing at a rate of 12% (Bergerud 1971). Differences in behavioral strategies toward lynx predation between the two herds and between male and female calves were proposed as explanations for much of the calf mortality and were thought to account for the relatively low growth rates of the herd (Bergerud 1971). It is known now that the Avalon herd also differed in being free of *E. rangiferi* at that time. It is also interesting to note that mean annual temperatures over the period of the decline from 1959-1962 were significantly warmer than the period from 1987-1997, during which no epizootic was seen ($\bar{x}$=4.7±0.3°C and $\bar{x}$=3.5±0.2°C, respectively; U=1, P=0.04). Considering these observations it is tempting to speculate that *E. rangiferi* may have been a major factor in this episode of high calf mortality recorded in the central part of Newfoundland and that lynx were simply feeding opportunistically on calves already stricken with CSE.

The most recent epizootic of CSE was seen in the Avalon herd beginning in January of 1996 (Lankester and Fong 1998). The impact of the disease on this herd was unusual. Sick animals with *E. rangiferi* were especially common. Over 100 were observed in the vicinity of Cape Race in the winter of 1997 (Con Finlay pers. comm.). The size of the herd dropped rapidly from an estimated 7,000 in 1995 to 1,845 in 1998 (Mahoney 2000). Notably, adult animals, as well as calves, showed signs of the disease. Few mature stags could be found during the most recent

census (Con Finlay pers. comm.). As in the earlier epizootic in central Newfoundland, this one seen in the Avalon herd probably was perpetuated by unusually warm, snow-free winters experienced on the Avalon Peninsula from 1995-1998. These conditions would have provided long transmission periods through the fall and winter when slugs remained available to caribou. Although the mean intensity and abundance of larvae passed did not differ between animals in the Avalon and the equally infected St. Anthony herd, reports of CSE and apparent mortality did.

The high rate of adult mortality and resulting precipitous decline in the size of the Avalon herd suggests that animals in this herd, particularly the adults, were unusually susceptible to disease caused by *E. rangiferi*. This I hypothesize, may be due to the parasite's recent arrival. There is now good evidence that the Avalon herd remained free of *E. rangiferi* until about 1990 (Lankester and Fong 1998; present study) whereas the parasite has existed for about 90 years in the other herds. Although the mean intensity and abundance did not differ between the Avalon and St. Anthony herds, the overall frequency of recently acquired worms in the cranium was higher in caribou of the Avalon (29%) than in St. Anthony herd (16%). As well, only caribou in the Avalon herd continued to acquire infection after they reached 2 years of age (6 out of 33 adult caribou had worms in the cranium) while none of 73 animals, 2 years and older, from other herds had recently acquired worms. These results suggest that caribou in herds that have existed for some time with this parasite and that had become infected as calves or yearlings, acquire a degree of protection against further infection. A similar acquired immunity seems to protect adult white-tailed deer from accumulating *P. tenuis* (Slomke et al. 1995). Older caribou in the Avalon herd, on the other hand, appear less able to resist infection. It might be argued that these animals (3-7 years of age) never encountered the parasite when they were calves, yet this seems unlikely, since high rates of

infections have been experienced by the herd for the last 5 years. Possibly, never having encountering the parasite before, this naive herd had a large number of individuals that were incapable of developing a protective immunity against reinfection, thus explaining continued adult mortality. A test of this hypothesis and evidence for the predicted future selection of immuno-competence to *E. rangiferi* will be a decline or absence of worms in the cranium and CSE in adult animals. Despite a possible increase in immuno-competence, the Avalon herd is unlikely to ever again show the previously observed high growth rates noted by Bergerud (1971) and Bergerud et al. (1983). The establishment of this parasite in what is climatically the best region in the Province for transmission, will likely continue to result in periodic epizootics of CSE in the calf cohort and herd growth no better than that seen elsewhere in the Province.

The dramatic decline seen recently in the Avalon herd is not unlike a much earlier one in the Interior herd described by Bergerud (1971). In the period between 1915 and 1930, the herd declined from an estimated 40,000 animals to 2,000. A loss of this magnitude, he reasoned, had to have been due to high rates of mortality in both adults and calves. It is interesting to note that this precipitous decline began less than a decade after the 1908 introduction of *E. rangiferi* to the Province of Newfoundland.

The abomasal nematodes *Ostertagia gruehneri* and *Trichostrongylus axei,* have previously been recorded from caribou and reindeer, however there is no known report of *Haemonchus contortus* (Mitskevitch 1929; Skrjabin et al. 1952; Dróżdż 1965; Bergerud 1971; Pryadko 1976; Leader-Williams 1980; Bye and Halverson 1983; Freutel and Lankester 1989). The presence of *H. contortus*, which is a common parasite of small ruminants, probably results from caribou grazing

around several coastal communities on the Avalon peninsula where sheep and goats range freely. This practice, however, is less common around St. Anthony.

Ostertagia gruehneri is the most common trichostrongyle infecting northern reindeer and caribou populations (Mitskevitch, 1929; Bergerud 1971; Pryadko 1976; Leader-Williams 1980; Bye and Halverson 1983; Bye 1987) and was the most abundant abomasal nematode (% of identified worms) in all caribou herds in Newfoundland. The infective third-stage larvae of *Ostertagia spp.* that accumulate on ground vegetation can survive freezing, an adaptation which may account for its dominance in more northerly areas (Tharaldsen 1976). Halverson et al. (1999) confirmed this survival strategy by demonstrating that *O. gruehneri* is transmitted to reindeer year round including the winter months on Svalbard Island, Norway. *Trichostrongylus axei* which was least abundant in the more northerly herds of Newfoundland may not be as well adapted to colder climates. Infective stage larvae of *Trichostrongylus spp.* can survive well at cooler temperatures, but are susceptible to freezing (Dunn 1978).

Mean abomasal worm counts were highest in caribou herds located on the Avalon peninsula in southeastern Newfoundland, with the highest abundance in the Cape Shore herd (12,245 ± 2,470). Abundance declined toward the north. The St. Anthony herd, which is located at the northern tip of the province, had the lowest mean APC at 2,513 ± 281. The low worm burdens in calves were similar to that reported in reindeer calves examined on Svalbard Island, Norway (Bye and Halverson 1983; Halverson et al. 1999; Irvine et al. 2000).

Several climatic factors were correlated with mean intensity of abomasal worms. Herds in areas experiencing the warmest temperatures, highest precipitation and lowest annual snowfall had the greatest mean APC. There was no correlation between mean APC and herd density. This may

have been due to my inability to separate the possible effects of density from that of climate. For example, the St. Anthony herd which had the highest animal density and the lowest worm burden occupied the coldest and driest study area. Comparison between the Cape Shore and Avalon herds which have similar climates does support a positive trend between herd density and mean APC. In studies where a correlation between worm abundance and herd density was found, climatic variation between study sites may not have been as wide as seen among areas in Newfoundland. In the APC assessment by Eve and Kellogg (1977), white-tailed deer herds were examined from several areas in the southeastern U.S., a region known for its consistent warm, humid climate. As well the reindeer herds examined by Bye (1987) were in close proximity to each other within mountain tundra regions of southern Norway (61' 10°N). It seems then that climate may be important to trichostrongyle transmission by possibly altering the development and survival of larval stages.

Trichostrongylid nematodes have a monoxenous life cycle. The absence of an intermediate host in the trichostrongyle life cycle exposes the early developmental stages to direct environmental influence. Studies have shown that both temperature and moisture are strongly correlated with the development of the free-living stages of these nematodes (Ciordia and Bizzell 1963; Crofton 1957, 1971; Pandey, 1972; Boag and Thomas 1977). Of the free-living stages, the infective third-stage larvae is the most resistant to adverse climatic conditions. These larvae adapted to withstand dessication and temperatures below freezing as a survival mechanism (Crofton 1971; Grenfell et al. 1986). Eggs and pre-infective larvae (first and second stage) are highly susceptible to extreme temperature fluctuations and dessication (Pandey 1972; Freutel 1987). Thus, it is advantageous for development to proceed to the infective third-stage quickly.

Unlike *E. rangiferi*, the accessability of infective stage trichostrongyle larvae to caribou is not dictated by intermediate host movement. These larvae move onto the vegetation where they remain, with some species available for year round transmission (Halverson et al. 1999). It would seem then that the importance of temperature variables influencing mean APCs among herds relates more to reduced larval survival than to length of transmission period. The influence of climate on larval development is well documented (Goldberg 1968; Michel 1976; Randall and Gibbs 1977). Warm, wet conditions during the summer months enhance numbers of larvae emerging from feces and increase herbage contamination. In contrast, cooler, drier conditions reduced larval development and movement, consequently reducing transmission. The developmental sensitivity of larvae to climate, may provide an explanation for the low APC in more northerly herds, especially those with higher animal densities.

The method of using APCs to monitor herd density in this report was inadequate due to the influence of climate on parasite transmission. The success of its use in other studies seems to rely on climate stability between study sites. Further examination is needed to confirm our findings, however, it is apparent that climatic influence should be considered before abomasal worm counts are employed as a management tool.

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