Factors affecting the distribution and transmission of *Elaphostrongylus rangiferi* (Protostrongylidae) in caribou (*Rangifer tarandus caribou*) of Newfoundland, Canada

Mark C. Ball, Murray W. Lankester, and Shane P. Mahoney

Abstract: *Elaphostrongylus rangiferi* was introduced to caribou (*Rangifer tarandus caribou*) of Newfoundland by infected reindeer (*R. t. tarandus*) from Norway and has caused at least two epizootics of cerebrospinal elaphostrongylosis (CSE), a debilitating neurologic disease. In an attempt to understand the conditions necessary for such outbreaks, we examined the effects of herd density and climatic factors on parasite abundance. The abundance of *E. rangiferi* was represented by counts of first-stage larvae in feces collected from young caribou (calves and yearlings) in 7 distinct caribou herds in Newfoundland. Abundance of *E. rangiferi* was highest in February and in the Avalon (632 ± 14 (mean ± SE)) and St. Anthony (526 ± 145) herds, the 2 herds in which CSE was most frequently reported. Mean abundance in February samples from young animals correlated positively with mean annual minimum temperature (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). Results suggest that abundance of *E. rangiferi* and the likelihood of cases of CSE are increased by moderate summer temperatures suitable for the activity and infection of gastropod intermediate hosts and by mild winters with little snow that extend the transmission period. Abundance of larvae was not correlated with herd density. Animals in all 7 herds also had the muscle worm *Parelaphostrongylus andersoni*, a related nematode with similar dorsal-spined larvae. In 2 additional herds (Cape Shore and Bay de Verde), *P. andersoni* occurred alone and larvae were passed only by young caribou. In herds with dual infections, numbers of *P. andersoni* larvae were depressed, declined more quickly in young animals, and were considered to be present in only low numbers in February samples used for *E. rangiferi* analysis. Upon initial infection, young caribou develop a resistance to *E. rangiferi* that prevents or reduces reinfection later in life. This was demonstrated by examining the brains of caribou for recently acquired worms, which must develop there for up to 90 days before continuing their tissue migration into the skeletal muscles. Recent infections were detected in only calves and yearlings in all herds with *E. rangiferi* except the Avalon herd, where developing worms were also found on the brains of older caribou. The infection of older animals in the Avalon herd may reflect a lower immunocompetence of a naive herd that has only recently been exposed to *E. rangiferi*.

Résumé : *Elaphostrongylus rangiferi* a été transmis aux Caribous (*Rangifer tarandus caribou)* de Terre-Neuve par des Rennes (*R. t. tarandus)* de Norvège infectés et a causé au moins deux épidémies d'élaphostrongylose cérébrale (CSE), une maladie neurologique débilitante. Pour mieux comprendre les conditions nécessaires à de telles épidémies, nous avons examiné les effets de la densité élevée des caribous dans la horde et des facteurs climatiques sur l'abondance des parasites. L'abondance des parasites a été évaluée par dénombrement des larves de premier stade dans les fèces de jeunes caribous (jeunes de 1 an ou moins) de 7 hordes distinctes de Terre-Neuve. L'abondance moyenne d'*E. rangiferi* s'est avérée maximale en février chez les hordes d'Avalon 632 ± 14 (moyenne ± écart erreur)) et de St. Anthony (526 ± 145), les deux hordes où la CSE a été le plus fréquente. L'abondance moyenne dans les échantillons de jeunes animaux en février était en corrélation positive avec les températures minimales moyennes annuelles (r_S = 0,829, dl = 6, P = 0,04) et avec le nombre de jours à température supérieure à 0°C dans l'année (r_S = 0,812, dl = 6, P = 0,05) et en corrélation négative avec les températures moyennes d'été (r_S = –0,830, dl = 6, P = 0,04). Les résultats indiquent que l'abondance d'*E. rangiferi* et la probabilité des élaphostrongyloses sont accrues par des températures estivales modérées propices à l'activité et à l'infection des gastropodes hôtes intermédiaires, de même que par des hivers doux avec peu de neige, qui prolongent la période de transmission. L'abondance des larves n'était pas reliée à la densité du troupeau. Les animaux des 7 hordes étaient également porteurs du parasite musculaire *Parelaphostrongylus andersoni*, un

Received October 23, 2000. Accepted May 10, 2001. Published on the NRC Research Press Web site at http://cjz.nrc.ca on July 12, 2001.

M.C. Ball and M.W. Lankester.[1] Department of Biology, Lakehead University, Thunder Bay, ON P7B 5E1, Canada.
S.P. Mahoney. Government of Newfoundland and Labrador, Department of Wildlife and Agrifoods, St. John's, NF A1B 4J6, Canada.

[1]Corresponding author (e-mail: murray.lankester@lakeheadu.ca).

 DOI: 10.1139/cjz-79-7-1265

nématode apparenté, dont les larves ont aussi des épines sur le dos. Chez 2 autres hordes (Cape Shore et baie de Verde), *P. andersoni* était seul présent et les larves n'étaient transmises que par des jeunes caribous. Chez les hordes hôtes des deux parasites, le nombre de larves de *P. andersoni* était réduit et il diminuait plus rapidement chez les jeunes animaux; les parasites de cette espèce n'étaient présents qu'en petits nombres dans les échantillons de février utilisés pour l'analyse d'*E. rangiferi.* Au moment de l'infestation initiale, les jeunes caribous développent une résistance à *E. rangiferi* qui prévient les réinfections ultérieures ou en diminue la gravité. Nous avons pu le démontrer en examinant des cerveaux de caribous pour y repérer les vers acquis depuis peu et qui doivent rester dans les cerveaux pour au moins 90 jours avant de continuer leur migration tissulaire jusqu'aux muscles squelettiques. Les nouvelles infections n'ont été observées que chez les nouveau-nés et les animaux de 1 an chez toutes les hordes hôtes d'*E. rangiferi*, sauf chez la horde d'Avalon où des vers en développement ont été trouvés aussi chez des caribous adultes. La présence d'infections chez des caribous plus âgés à Avalon s'explique peut-être par la compétence immunitaire plus faible qui prévaut chez une horde « naïve » qui n'a été exposée que récemment à la présence d'*E. rangiferi.*

[Traduit par la Rédaction]

Introduction

Elaphostrongylus rangiferi Mitskevich, 1958 is a common parasite of semidomesticated and wild reindeer (*Rangifer tarandus tarandus*) in northern Fennoscandia and Russia (Halvorsen 1986*a*). It is responsible for periodic epizootics of a debilitating neurologic disease seen primarily 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 in the reindeer industry during epizootics because of winter deaths, unthriftiness, forced culling for slaughter, and carcass trimming (Lankester 2001). 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 Fennoscandia has been diminished by the widespread use of ivermectin (Stéen et al. 1998; A. Oksanen, personal communication). It is not feasible, however, to use this method of control in wild cervids such as caribou (*R. t. caribou*) in Newfoundland, Canada, where *E. rangiferi* was introduced with infected reindeer from Norway in 1908 (Lankester and Fong 1989).

First-stage, dorsal-spined larvae (L1) of *E. rangiferi* are passed in the feces of infected caribou and penetrate the foot of terrestrial gastropod intermediate hosts, where they develop to the infective third-stage larva (L3) (Halvorsen 1986*a*). New infections result when infected snails and slugs are accidently ingested with food. L3 migrate to the central nervous system (CNS), where they develop to the adult stage in about 90 days before moving to their definitive site among skeletal muscles (Hemmingsen et al. 1993).

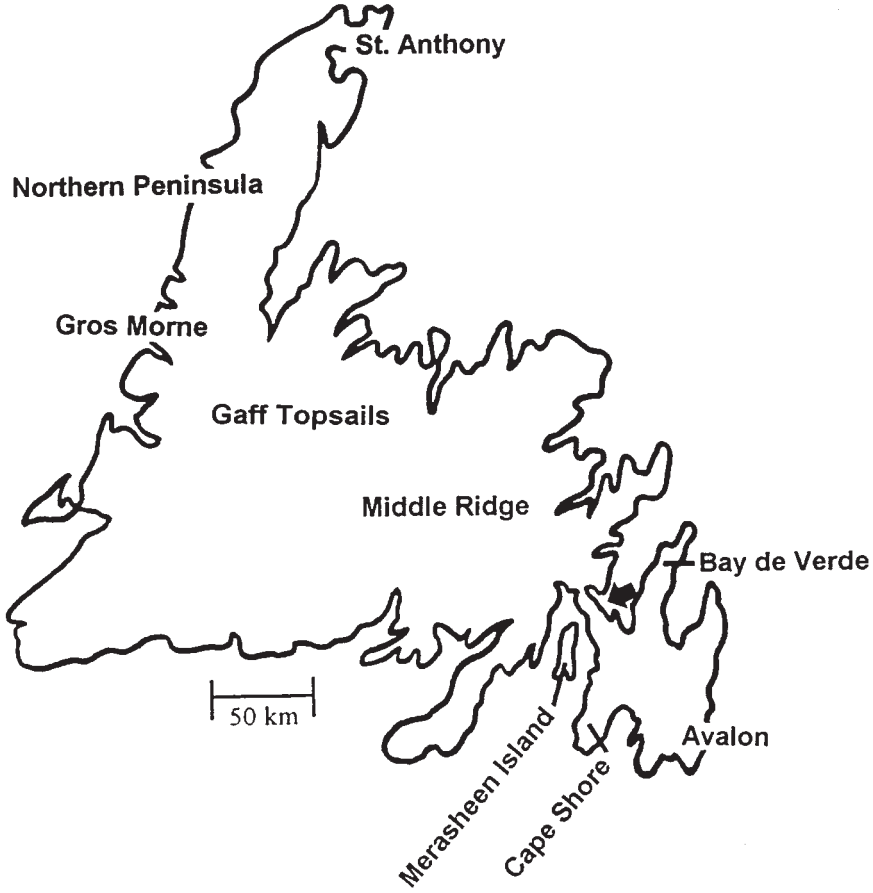
The severity of elaphostrongylosis appears to be dose-dependent (Halvorsen 1986*b*). Animals acquiring relatively few L3 may show no outward signs of disease and only experience a subclinical verminous pneumonia (Lankester 2001). Those ingesting moderate numbers of the parasite often separate from the herd, stay in one place for an extended period, and appear "stunned" or unusually tame. Reindeer and caribou acquiring the heaviest infections 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). This most severe manifestation of the disease is known as cerebrospinal elaphostrongylosis (CSE) and is seen most frequently in young male animals from January to March, but may be observed at any time of the year. Males are differentially affected because they eat more and likely ingest more L3 (Halvorsen 1986*b*).

Periodically, an unusually large number of animals exhibit CSE. Two verified epizootics have occurred in caribou since the recognition of the parasite in Newfoundland. The first occurred in the Buchans and Gaff Topsails areas of central Newfoundland in the early to mid-1980s (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 1996, 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 7000 animals to less than 2500 (Lankester and Fong 1998; Mahoney 2000). CSE was observed in calves and yearlings but also in adult animals.

Climatic conditions responsible for epizootics of CSE have been examined by Handeland and Slettbakk (1994) in northern Norway, where mean summer temperatures (June–August) average ca. 12°C. Seven late-winter outbreaks seen in reindeer 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 *E. rangiferi* L3 in gastropods, leading to heavier than usual late-summer and autumn infections in ruminants (Halvorsen 1986*a*).

In Newfoundland, the presence of *E. rangiferi* in several discrete caribou herds separated latitudinally provided an opportunity to examine the influence of various climatic factors as well as herd density on transmission of the parasite. The abundance of L1 in feces was taken to represent the level of *E. rangiferi* infection in animals of known or estimated age. This measurement, however, was potentially confounded by the presence in some herds of the muscle worm *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. It also has a shorter prepatent period (51 vs.120 days) and L1 that are shorter, on average, than those of *E. rangiferi* (Lankester and Hauta 1989). Finally, we also attempted to determine why old as well as young caribou were showing

Fig. 1. Map of Newfoundland, Canada, showing the areas occupied by the caribou (*Rangifer tarandus caribou*) herds from which hunter-killed caribou and fecal samples were collected: St. Anthony (51°N, 55°W); Northern Peninsula (50°N, 55°W); Gros Morne (49°N, 56°W); Gaff Topsails (49°N, 56°W); Middle Ridge (47°N, 53°W); Merasheen Island (47°N, 52°W); Avalon (46°N, 51°W); Cape Shore (46°N, 51°W); and Bay de Verde (48°N, 51°W). The arrow indicates the narrow isthmus separating the Avalon Peninsula from the rest of the island.



signs of CSE in the recently exposed Avalon herd, while only young animals appeared affected in herds where *E. rangiferi* has been established for almost a century.

Study herds and climate

Woodland caribou were examined from 9 discrete herds in Newfoundland: St. Anthony, Northern Peninsula, Gros Morne, Gaff Topsails, Middle Ridge, Merasheen Island, Avalon, Bay de Verde, and Cape Shore (Fig. 1). These herds occupied seven different ecoregions associated with different forest types and climatic conditions (Meades and Moores 1994). Herd densities estimated by aerial survey and telemetry between 1994 and 1999 (Mahoney 2000) ranged from 0.1 animal/km^2 in the Bay de Verde to 3.0 animals/km^2 in the Middle Ridge herd (Table 1). Canadian Climatic Service (Fredericton, N.B.) weather data taken in proximity to the main caribou herds during 1997 and 1998 varied by latitude (Table 1). 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 Peninsula 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 ca. 60 fewer days with temperatures above 0°C, mean annual temperatures ca. 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 higher and approximately 15 more days with temperatures above 0°C than adjacent areas to the south.

Methods

Thirty fecal pellets and the head, including the jawbone, were collected from each caribou killed by hunters or vehicles between September 1998 and February 2000. The entire CNS and skeletal musculature were examined for *E. rangiferi* when whole carcasses of road-killed and sick animals were available. Caribou were aged by tooth eruption and wear pattern (Miller 1972). Sex, date of kill, and location were recorded. Parasite identifications were based on the morphometrics of adult male worms from caribou as well as dimensions of L1 recovered from feces.

Additional fecal samples comprising 20–30 pellets from each of approximately 30 animals were collected from the ground at each of the study sites in September, December, and February of each year and from the more accessible Avalon herd almost every month. The size of these pellets was used to estimate the age of the animals that produced them, providing a convenient way of increasing age-specific sample sizes. Dimensions of pellets from known-age animals established that pellets from calves and year-

Table 1. Canadian Climate Service (CCS) weather data recorded in proximity to caribou (*Rangifer tarandus caribou*) herds in Newfoundland and estimated herd densities.

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. of days >0°C	Mean no. of days >10°C	Herd density[c] (animals/km^2)
St. Anthony	960	240	1200	0.5	6.8	2.5	275	117	2
Northern Peninsula	1002	397	1399	–2	6.6	2.8	262	147	0.6
Gros Morne	586	224	810	–2	6.5	2.2	259	141	0.7
Gaff Topsails	1038	310	1348	0.2	7.7	3.9	275	146	1.8
Middle Ridge	1222	186	1408	0.6	8.4	4.8	271	153	3
Merasheen	1249	172	1421	1.1	8.5	5.1	290	165	2.6
Avalon	1293	145	1438	1.2	8.8	5.4	305	155	0.5
Cape Shore	1225	166	1391	2	8.9	5.5	316	162	2.4
Bay de Verde	1002	179	1181	1	10	5.5	326	169	0.1

[a]Location of climatological station closest to the herd ranges in order beginning from St Anthony: Flower's Cove (CCS Station No. 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]Mean for the years 1997 and 1998.
[c]Data are from Mahoney (2000).

lings (<1.4 cm long) were significantly shorter than those from animals 2 years and older (U = 5014, P = 0.001) (Ball 2000). Hence, pellets designated as small and collected directly off range in September and December were considered to have been deposited by young animals, including calves 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.

Pellets were placed in plastic sample bags and kept frozen at –20°C for ≤ 1 month before being thawed and examined at Lakehead University, Thunder Bay, Ontario. All fecal samples were examined for L1 using the modified Baermann-beaker method (Forrester and Lankester 1997). Numbers of extracted L1 are expressed as larvae per gram of dried fecal material. Mean lengths of L1 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 40× using a drawing tube.

Heads from known-age hunter-killed caribou were examined to detect recently acquired *E. rangiferi* infections. Animals ingesting L3 within the past 90 days will have developing worms in the pia-arachnoid membrane covering the brain (Hemmingsen et al. 1993). The skull cap was removed using a bone saw, the brain was removed, and the cranium and brain surfaces were inspected visually. The locations of grossly visible worms were recorded. Worms were counted and fixed in 70% ethanol 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 membrane, was removed with a sharp scalpel, pressed between two heavy glass plates (4.5 × 4.5 cm), and examined for any remaining worms by means of a stereomicroscope at 16–24×.

Data were analyzed using the Statistical Package for the Social Sciences (SPSS), version 9.0 (SPSS Inc., Chicago). Non-parametric statistical tests were used, as we were unable to achieve homogeneity of variance by data transformation. Comparisons of mean larval intensities and abundances between years, 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 regard to age and sex of caribou host. Chi-squared analysis was used to detect differences in the prevalence of infection (%) and the frequency of migrating worms in the cranium among herds, ages, and seasons. Spearman's rank correlation tests were used to examine relationships between numbers of adult worms in the skeletal musculature and mean intensity of larvae produced and abundance of *E. rangiferi* in relation to herd density and climatic variables.

Results

Larval dimensions

The mean length of L1 passed in the feces of caribou varied in relation to herd, age of caribou, and sampling time (Table 2). Overall, the mean lengths of L1 passed by caribou of the Cape Shore and Bay de Verde herds were significantly less than those from all other herds (U = 9287, P < 0.001, and U = 4938, P < 0.001, respectively) and resembled those of *P. andersoni* larvae. These larvae never exceeded 400 μm in length and occurred during all 3 sampling periods but only in small fecal pellets considered to be from calves or yearlings. Only adult *P. andersoni* were recovered from the musculature of caribou from the Cape Shore and Bay de Verde herds and all L1 in feces from these 2 herds were considered to belong to this species only (Tables 2–5).

Table 2. Lengths (μm) of dorsal-spined larvae[a] from the feces of Newfoundland caribou.

	September			December			February		
Herd	Small	Large	Total	Small	Large	Total	Small	Large	Total
St. Anthony	344 ± 4 (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)
Northern 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)

Note: Values are given as the mean ± SE with the range in parentheses. Measurements are from 30 larvae pooled from samples examined.
[a]Small, pellets with mean length ≤1.4 cm; large, pellets with mean length >1.4 cm.

The remaining 7 herds were considered to have mixed infections, since larvae of two different sizes were being passed. The mean lengths of L1 in small pellets in September did not differ from those in the Cape Shore and Bay de Verde herds, indicating that most were probably *P. andersoni*. However, significantly longer L1 occurred in the 7 herds in December (H = 8.13, P = 0.04) and February (H = 10, P = 0.03) samples. The longer L1 reached 470 μm and resembled those of *E. rangiferi*. The mean length of L1 in large pellets was greater than the length of those in small pellets during each sampling period (September: U = 605, P < 0.01; December: U = 4001, P < 0.01; February: U = 8264, P < 0.01) but did not differ among the 7 herds at any time.

Prevalence and intensity

Fecal samples from hunter-killed animals

In fecal samples from 166 caribou killed by hunters, the overall prevalence of L1 ranged from 24% in the Middle Ridge herd to 76% in the Avalon herd (Table 3). Overall, the mean intensity of L1 differed among herds (H = 19, P = 0.002) but only during the autumn period (September and October) (H = 14, P = 0.02), with older males in the Merasheen herd passing the most. Only the Avalon herd showed an increase in L1 output from autumn to winter (November and December) (U = 174, P = 0.004). On average, male caribou tended to pass more L1 than females, 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 in the Avalon herd did yearlings pass 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 from caribou range during 3 sampling periods (September, December, and February) and from hunter-killed animals in September and December (Table 4). Prevalence and mean intensity data did not differ between sampling years (1998–1999 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. Yet mean intensity was highest in these herds (936 ± 166 and 2209 ± 505 (mean ± SE), respectively) (H = 56, P = 0.00) and only young animals were passing larvae.

In the 7 herds with mixed infections, overall prevalence of larvae in feces ranged from 40% in the Gaff Topsails herd (n = 83) to 83% in the Avalon herd (n = 135) (Tables 4 and 5). Mean intensity overall was greatest in the Gaff Topsails herd (446 ± 134) and lowest in the Middle Ridge herd (116 ± 33) and varied with season for all herds (H = 56, P = 0.00) except Middle Ridge. Overall, the highest intensities in both classes of pellets occurred in February. Mean intensity did not vary 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

Table 3. 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[a]	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Autumn										
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)	
Total for sex	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)	

Note: Intensity is expressed as the number of larvae per gram of dried feces (mean ± SE), with prevalence followed by the sample size in parentheses.
[a]Autumn, September 6 – October 31; winter, November 1 – December 31. Age-classes: 0, calves; 1, yearlings; 2+, 2–10 years of age.

Table 4. Mean intensities of dorsal-spined larvae in fecal pellets[a] of caribou in Newfoundland (collected from the ground and from animals killed by hunters).

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

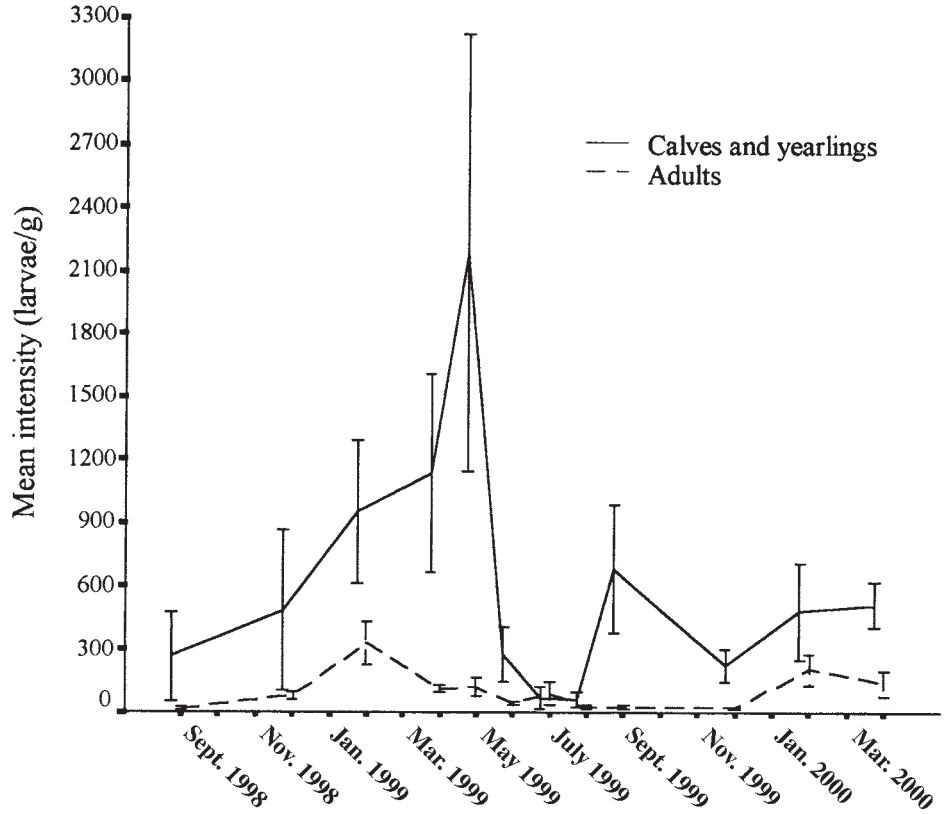
Note: Intensity is expressed as the number of larvae per gram of dried feces (mean ± SE), with the prevalence in parentheses. For sample sizes see Table 5.
[a]Small pellets have a mean length ≤1.4 cm; large pellets have a mean length >1.4 cm.

Table 5. Abundances of dorsal-spined larvae in fecal pellets[a] of caribou in Newfoundland (collected from the ground and from animals killed by hunters).

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

Note: Values are given as the mean ± SE with the number of animals infected followed by the sample size in parentheses.
[a]Small pellets have a mean length ≤1.4 cm; large pellets have a mean length >1.4 cm.

Fig. 2. Monthly intensities (mean ± 1 SE) of dorsal-spined larvae in the feces of caribou from the Avalon herd, Newfoundland.



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 from the ground every few months from September 1998 to April 2000. The prevalence of L1 was high in both small and large pellets throughout most of the year (80–100%) but declined somewhat during late summer (48–69%). Mean intensity did not differ significantly 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 (Fig. 2). Small pellets (from calves and yearlings) had higher numbers of L1 than large pellets (from adults) throughout the year. Larval numbers tended to peak in February in large pellets but continued to rise until 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 3012 and 5693 larvae/g.

Abundance of L1 by season, age, climate, and density among herds

Factors affecting abundance (prevalence × mean intensity) of all L1 passed by caribou were examined only in the 7 herds with mixed *E. rangiferi* and *P. andersoni* infections. Overall, there was a significant increase in the abundance of L1 from September to February in both small (H = 9, P < 0.01) and large (H = 37, P < 0.001) pellets (Table 5). Larval abundance in small pellets varied among herds in all 3 sampling periods (September: H = 10, P = 0.02; December: H = 18, P = 0.003; February: H = 19, 0.01) and in large pellets between September (H = 17, P = 0.001) and December (H = 15, P = 0.01) but not in February.

A Spearman's rank correlation analysis between mean larval abundance (for 1998–1999 and 1999–2000) and various weather parameters used only counts of L1 in small fecal pellets collected in February and mean annual weather data for 1997 and 1998. These two years spanned the period during which the young cohort of caribou examined here became infected. Only February data were used, since most *E. rangiferi* acquired the previous year would have been mature and passing larvae by this time and the numbers of *P. andersoni* L1 were thought to be at their lowest. 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). As well, the mean abundance of *E. rangiferi* was significantly lower in herds experiencing mean summer temperatures above 13°C than in herds at lower temperatures (r_S = 1.0, df = 6, P < 0.001). There was no significant correlation between parasite abundance and herd density (r_S = –0.143, df = 6, P = 0.79).

Recent infections by age

Immature *E. rangiferi* were present on the brains of 38%

Table 6. Prevalence (%) of *Elaphostrongylus rangiferi* on the brains of hunter-killed caribou from different herds in Newfoundland.

Age (years)[a]	Avalon	Cape Shore	Middle Ridge	Merasheen	St. Anthony	Gaff Topsails	Total
0	83 (5/6)	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)
Total	29 (15/52)	0 (0/39)	4 (1/24)	4 (1/26)	16 (5/32)	5 (1/19)	12 (23/190)

Note: Values in parentheses show the number of animals infected/examined; most had 1 or 2 worms, but 5 calves (3 from the Avalon herd and 2 from the St. Anthony herd) each had 12.

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

Table 7. Intensity of adult *E. rangiferi* and dorsal-spined larvae from caribou of known age and sex.

Area of collection	Date of collection	Sex	Approx. age (months)	No. of adult worms in muscle	No. of larvae/g of dried feces
Gaff Topsails[a]	5 Feb. 1984	F	9	6	29
	28 Jan. 1984	F	9	5	6
	21 Mar. 1984	F	10	14	121
	20 Mar. 1984	F	10	18	41
St. Anthony	14 Dec. 1998	M	19	21	310
Avalon	20 Nov. 1998	M	19	83	2090
Avalon	6 Jan. 1999	F	20	46	1298

[a]Data from Fong (1984).

of 45 calves and yearlings examined from 5 herds (Table 6). None was found on the brains 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 crania 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 crania of 39 caribou examined from the Cape Shore herd, where only *P. andersoni* occurs.

Adults versus first-stage larvae of *E. rangiferi* in feces

The total number of adult *E. rangiferi* in the musculature and head of infected caribou was correlated with the mean intensity of larvae passed in the feces ($r_S = 0.976$; $n = 7$) (Table 7).

Discussion

Both *E. rangiferi* and *P. andersoni* were found in 7 of the 9 caribou herds studied. Only *P. andersoni* infected the Cape Shore and Bay de Verde herds. This parasite is known to occur widely in woodland and barrenground caribou across North America (Lankester 2001), whereas Newfoundland is the only place in North America where *E. rangiferi* has been found. It took ca. 80 years for *E. rangiferi* to spread from St. Anthony at the northern tip of Newfoundland, where Norwegian reindeer were first introduced, 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 (Fig. 1). The conclusion by Lankester and Fong (1998) that *E. rangiferi* did not reach the Avalon herd until ca. 1990 is further corroborated by the fact that the Cape Shore and Bay de Verde herds are free of it and both were established by translocating animals from the Avalon herd in 1977 and 1989, respectively (Finlay and Oosenbrug 1984; S.P. Mahoney, unpublished data).

The 2 herds infected with only *P. andersoni* showed that when this parasite occurs alone in caribou, numbers of L1 reach very high levels in February but are passed only by young animals, indicating that most adult worms are probably overcome before animals reach 2 years of age. This is consistent with the findings of Lankester and Fong (1998), who recovered adult and larval *P. andersoni* from 7- to 13-month-old caribou of the Middle Ridge herd but not from 19-month-olds 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* L1 (13/g of fresh feces), but calves and yearlings similarly passed the most, and in the spring (March and early April). Infections in the Beverly herd differed in that small numbers of L1 continued to be produced by older caribou, although this may have been a function of lower infecting doses or a later sampling time (March–April vs. February in the present study). Experimental studies indicate that larval production by *P. andersoni* in caribou and white-

tailed deer (*Odocoileus virginianus*) rises quickly after patency, to peak in 2–8 weeks, and then declines (Nettles and Prestwood 1976; Pybus and Samuel 1981; Lankester and Hauta 1989).

Monthly collections of pellets from the Avalon herd, where animals had both *P. andersoni* and *E. rangiferi*, provided an opportunity to estimate changes in the proportions of L1 produced by each in relation to season and caribou age. L1 produced by older caribou in February were likely exclusively those of *E. rangiferi* and the peak in numbers seen each year at this time probably represented the "spring rise" that occurs in many related nematodes (Prosl and Kutzer 1980; Samuel et al. 1985; Lankester and Hauta 1989; Slomke et al. 1995). Larval output by young animals peaked in September and then again in February through to May. As the smaller pellet class contained several new calves infected over summer, the peak in September was probably due mostly to *P. andersoni*, which requires only 51–66 days to become patent (Lankester 2001). The second peak seen from February to May would have also included L1 of *E. rangiferi*, which requires 4–4.5 months to become patent (Handeland et al. 1994). The presence of both species in February samples is reflected by the increased lengths of Ll in February (406 ± 6 μm (mean ± SE), range 344–450 μm) over those in September (343 ± 4 μm, range 290–380 μm). The L1 of *P. andersoni* are shorter (358 ± 16 μm; range 319–385 μm) (Prestwood 1972; Lankester and Hauta 1989) than those of *E. rangiferi* (421 ± 13 μm; 370–445 μm) (Lorentzen 1979).

When *E. rangiferi* and *P. andersoni* occurred in the same host, the total output of L1 in February was reduced to one-half or one-third of that produced by animals infected with *P. andersoni* only. This suggests that an immunologically based interaction occurs between the two species. Because of the greater mean length of larvae passed in February, larval production by *P. andersoni* also appeared to drop off more quickly in mixed infections than when it occurred 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 parasite species 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 mixed infections appears to be greatly reduced.

In 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 elaphostrongyline nematodes, including white-tailed deer with *Parelaphostrongylus tenuis* (Anderson 1963; Slomke et al. 1995) or *P. andersoni* (Nettles and Prestwood 1976) and mule deer with *Parelaphostrongylus odocoilei* (Samuel et al. 1985). There was no significant difference in the numbers of L1 passed by adult male and female caribou, but adult males passed more in winter than males in autumn. This contrasts with a report by Halvorsen et al. (1985), who found an increase in larval output by male reindeer in autumn corresponding to the rut and by females in the spring prior to calving. 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).

In an attempt to identify factors important in the transmission of *E. rangiferi* and that might serve to predict outbreaks of CSE, we excluded some samples from the analysis and made certain assumptions. Only L1 counts in pellets collected from young caribou in February from the 7 herds with mixed infections were used. Although all L1 being passed by older caribou were probably *E. rangiferi*, these animals had been largely immune to re-infection since they were 2 years old (see later discussion), and any relationship between numbers of L1 passed and numbers of adult worms present may have been masked by a number of age- and immunity-related factors (Slomke et al. 1995). It was assumed that L1 in the pellets of young animals in February were mostly *E. rangiferi*. This was supported by the fact that the greater mean length of L1 in February samples coincided with the expected patency of *E. rangiferi* picked up by calves the previous autumn, a spring increase in the production of L1 by yearlings, and the failure of Lankester and Fong (1989) to find any adult *P. andersoni* in caribou 19 months of age and older. Lastly, we also concluded that the number of adult worms in caribou was reflected by counts of L1 passed in feces. This was supported by the positive correlation between the mean number of L1 passed and number of adult *E. rangiferi* in caribou. A similar relationship was demonstrated by Pybus and Samuel (1984) for *P. andersoni* in white-tailed deer, but was not found by either Bogacyzk (1990) or Slomke et al. (1995) for *P. tenuis* in this host. Despite the recognized limitations of some of these assumptions, we suggest that counts of L1 produced by calves and yearlings in February provide the best available approximation of the numbers of adult *E. rangiferi* in these animals and thereby reflect the relative suitability of conditions for transmission of the parasite over the preceding few years. Since the severity of elaphostrongylosis is thought to be related to the number of infective larvae ingested (Halvorsen 1986*b*), the identification of factors promoting transmission should enhance our ability to predict epizootics of CSE.

The mean abundance (prevalence × mean intensity) of L1 was considered to provide the best measure of the level of infection in the different herds and to reflect the average number of adult *E. rangiferi* acquired by calves and yearlings over the previous two summers. Mean abundance was also considered a reasonable measure of the numbers of larvae being shed onto caribou range and contributing to future infections. It was positively correlated with the number of days with maximum temperature above 0°C, ranging from 259 and 262 days in the vicinity of the Gros Morne and Northern Peninsula herds, respectively, to 305 in the area occupied by the Avalon herd. Abundance was also correlated with mean annual minimum air temperatures and was significantly lower in herds experiencing mean summer temperatures above 13°C than in herds at lower temperatures, suggesting that maximum abundance occurs at moderate summer temperatures.

Temperature may have its greatest effect on parasite abundance by influencing movement of gastropods on vegetation, which affects the likelihood both of their becoming infected and of being accidentally eaten by caribou. The principal inter-

mediate host of *E. rangiferi* in Newfoundland is *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 high up on ground vegetation during cool wet periods. It remains active at temperatures approaching freezing and is one of the first species to become 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 during which *D. laeve* is active and likely approximates the length of the annual transmission period for *E. rangiferi*. Peterson et al. (1996) similarly found a correlation between the prevalence of *P. tenuis* in white-tailed deer and the interval in autumn before snowfall when gastropods could still be ingested with food.

Temperature is known also to affect the survival and rate of development of larval *E. rangiferi* in gastropods. Survival of second-stage larvae may be diminished at lower temperatures (Schjetlein and Skorping 1995), but infective larvae certainly survive in gastropods over winter (Skorping and Andersen 1991). Almost no larval development occurs in gastropods at temperatures below 10°C (Halvorsen and Skorping 1982; Bodnar 1998[2]). At 14°C, 17% of *E. rangiferi* in *D. laeve* reached the infective stage in 6 weeks and all were L3 by 10 weeks (Bodnar 1998[2]). In the present study, the average annual number of days above 10°C ranged from a low of 117 days in the north at St. Anthony to 155 (32% more) in the area occupied by the Avalon herd in the south. However, since no correlation was observed between the abundance of *E. rangiferi* in the different herds and the number of days above 10°C, we conclude that abundance is not limited by temperatures required for the timely development of larvae to the infective stage. Higher than average summer temperatures have been associated with epizootics of CSE in reindeer and small ruminants in northern Norway (Halvorsen et al. 1980; Handeland and Slettbakk 1994, 1995). At higher temperatures, larvae were presumed to reach the infective stage faster over the relatively short summers, with 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, but in Newfoundland, at about 49°N and with a strong maritime influence, summers are 4–5 months long. Here, moderate summer temperatures and mild winters with little snow that extend the transmission period seem to be more important in maximizing the abundance of *E. rangiferi* and may be better predictors of epizootics of CSE.

An extended season for transmission may explain the two epizootics observed previously in Newfoundland. The one occurring in the Gaff Topsails area 1981–1985 spanned 5 years with significantly higher annual temperatures (4.1 ± 0.5°C (mean ± SE); $U = 4$, $P = 0.03$) and significantly lower total annual snowfall (167 ± 11 cm (mean ± SE); $U = 0$, $P = 0.003$) than in the following 11 years (1987–1997) (2.8 ± 0.2°C and 387 ± 21 cm, respectively), when few sick animals were reported. A series of unusually warm, snow-free winters also occurred on the Avalon Peninsula from 1995 to 1998, beginning just prior to the epizootic first noticed in 1996.

We found no correlation between herd density and the abundance of *E. rangiferi* in the 7 herds with mixed infections. Nor was caribou density the principal determinant of abundance of *P. andersoni* where it occurred alone. The Bay de Verde herd had more than twice the abundance of *P. andersoni* L1 than seen in the Cape Shore herd despite a much lower caribou density. Intuitively, parasite transmission rates and abundance will increase with host density, but this has been difficult to demonstrate without controlling for a variety of confounding factors (Arneberg et al. 1998) and without good estimates of host density. Quality estimates are particularly difficult to obtain for gregarious caribou, which segregate seasonally by sex and whose habitat-use patterns change over time (Thomas 1998). Other studies of protostrongylids have also failed to reveal 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), largely because an immunologically determined threshold number of adult worms is reached and no more are acquired beyond the age of 2 years (Slomke et al. 1995). For example, deer at two markedly different densities (2 and 30 animals/km^2) had similar numbers of adult *P. tenuis*. But for unknown reasons the deer at the higher density, nonetheless, were passing significantly more larvae. Peterson et al. (1996) did find that the prevalence of *P. tenuis* larvae in feces was correlated with deer density, but numbers of adult worms were not examined. Unraveling the relationship between abundance of *E. rangiferi* L1 and caribou density awaits, among other things, a better understanding of seasonal and annual changes in range use by these animals and their immunological responsiveness in relation to nutrition and concurrent parasite infections.

The recent epizootic of CSE in the Avalon 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, personal communication). The size of the herd dropped rapidly and, most notably, adult animals, as well as calves, showed signs of the disease (Lankester and Fong 1998). Few mature stags could be found during the most recent census (Con Finlay, personal communication). The high frequency of CSE and the precipitous decline in numbers of adult caribou suggest that this herd was unusually susceptible to *E. rangiferi*, possibly because of 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 of *E. rangiferi* did not differ between the Avalon and St. Anthony herds, the overall frequency of recently acquired worms in the cranium was higher in Avalon animals (29 vs. 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

[2] T. Bodnar. 1998. Development and survivorship of *Elaphostrongylus rangiferi* at different temperatures in the slug, *Deroceras laeve*. B.Sc.(Hons.) thesis, Lakehead University, Thunder Bay, Ont.

had worms in the cranium), while none of 73 animals 2 years of age and older in other herds had recently acquired worms. These results suggest that caribou in herds that have existed for some time with *E. rangiferi* acquire a degree of immunity following exposure as calves or yearlings and have some protection against further infection. A similar acquired immunity seems to protect adult white-tailed deer from accumulating *P. tenuis* (Slomke et al. 1995). One could argue that adult animals (3–7 years old) in the Avalon herd remained susceptible because they never encountered the parasite as calves, yet this seems unlikely, since high rates of infections have now been experienced by the herd for at least the past 5 years. Instead, we suggest that, as a naive herd, it originally included individuals that were incapable of developing sufficient protective immunity against reinfection, and still does, thus explaining the continued infection and mortality of adult animals. A test of this hypothesis and evidence for selection of increased immunocompetence to *E. rangiferi* will be a future decline or absence in adult animals of worms in the cranium and of CSE. It is tempting to suggest that a similar herd immunological naivety may in part explain a caribou decline (from an estimated 40 000 to 2000 animals) that occured in central Newfoundland between 1915 and 1930 (Bergerud 1971), beginning less than a decade after the arrival of *E. rangiferi* from Norway. If our hypothesis is correct, similar declines with high adult mortality can be expected when the parasite reaches the as yet unexposed Cape Shore and Bay de Verde herds.

Despite a predicted future increase in immunocompetence, the Avalon herd may never again show the high growth rates noted by Bergerud (1971) and Bergerud et al. (1983). With the establishment of this parasite in what is climatically the best region for transmission in the province, the Avalon herd will likely continue to experience periodic CSE epizootics, primarily involving calves, and herd growth will be similar to that seen elsewhere in the province.

Acknowledgments

We thank the Government of Newfoundland and Labrador Department of Wildlife and Agrifoods for providing financial assistance and Dr. Hugh Whitney and Christine Doucet for continuing advice and technical assistance. We gratefully acknowledge the field assistance and companionship of Barry Adams, Rick Curran, Mark Lawlor, Dave Slade, Eric Sullivan, and Harvey Thomas. We particularly thank Mr. Con Finlay for his countless contributions to this research.

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