Distribution of *Angiostrongylus vasorum* and *Crenosoma vulpis* in red foxes (*Vulpes vulpes*) in Newfoundland, Canada

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A thesis presented in partial fulfilment of
the requirements for the degree of Master of Science

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Abstract

Angiostrongylus vasorum, the French heartworm, and *Crenosoma vulpis*, a lungworm, infect the pulmonary arteries and the bronchi and bronchioles, respectively, of red foxes *(Vulpes vulpes*). Both are widespread in Europe, but within North America the distribution of *A. vasorum* is limited to the island of Newfoundland, Canada. During 2000-2002, 366 fox carcasses were collected from 6 regions of the island. This study is unique in being the first large-scale survey of *A. vasorum* and *C. vulpis* in a natural fox population. Its objectives were to determine the precise distribution of both parasites in Newfoundland and to examine the possibility of interaction between them.

Crenosoma vulpis occurred in all 6 regions at an overall prevalence of 87% and a mean intensity of 230 ± 20.8 (mean ± S.E.). Young-of-the-year foxes had higher mean intensities (260 ± 39.4) than yearlings (91 ± 31.2) or adults (78 ± 41.1) ($F_{[2, 153]} = 11.07, p < 0.001$). The intensity of *C. vulpis* was not related to host sex, omental fat ratio, or body fat index. There was a weak positive relationship between number of adult worms and output of first-stage larvae in feces ($r^2 = 0.199$, $F_{[1, 135]} = 34.84, p < 0.001$); larval output decreased with increasing fox age ($F_{[2, 127]} = 18.99, p < 0.001$).

Angiostrongylus vasorum occurred only in the 3 southeast regions of the island: the Avalon Peninsula, the North East Coast, and the South Coast/Burin Peninsula. Its distribution may be limited by cold temperatures as it did not occur in areas where mean winter temperatures were lower than −4°C. The prevalence was 56% and mean intensity 72 ± 7.6. The number of adult worms did not differ with host age, sex, omental fat ratio, or body fat index. Although

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named the French heartworm, 88% of all *A. vasorum* were recovered from the pulmonary arteries while the remainder were in the right ventricle. However, 78% of infected foxes had at least one worm in the right ventricle. Although the number of *A. vasorum* did not differ between the pulmonary arteries of the left and right lobes ($F_{[1, 164]} = 1.70, p = 0.194$), there were more worms in the arteries of the posterior lobes (47 ± 5.4) than in the anterior (24 ± 2.5) ($F_{[1, 161]} = 13.39, p < 0.001$). Also, there were no relationships between the number of *A. vasorum* and larval output, heart weight ratio, or ventricular ratio.

Although 40% of foxes from the *A. vasorum* positive regions had both *A. vasorum* and *C. vulpis* infections, there was no interaction between the two parasites ($G_{c[1]} = 0.10$). Furthermore, there was no linear relationship between the two parasites, and the mean intensity of each nematode did not differ between single and dual infections.

Eight coyotes (*Canis latrans*) from Newfoundland were also examined. None had *A. vasorum*, but 38% had *C. vulpis*, although the mean intensity (16 ± 10.2) was lower than that in foxes.

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I would like to extend my gratitude and thanks to Mike McGrath and everyone at the Provincial Wildlife Lab, Newfoundland Inland Fish and Wildlife Division, of the Department of Tourism, Culture, and Recreation, and to Dr. Hugh Whitney and laboratory staff of the Animal Health Division, of the Department of Forest Resources and Agrifoods, who provided me with the means and technical support necessary to complete this project. Also, thank you to Con Finlay, Spencer Cutler, and Mac Pitcher for all your help collecting carcasses.

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Introduction

Two metastrongyloid nematodes, *Crenosoma vulpis* (Dujardin 1844) and *Angiostrongylus vasorum* (Baillet 1866), parasitize red fox (*Vulpes vulpes*) in Newfoundland, Canada (Smith and Threlfall 1973, Whitney 1998). Both are zoonotic and can infect domestic dogs. They are widely distributed in wild and domestic canids of Europe (Anderson 2000), but *A. vasorum* is not established anywhere in North America outside of Newfoundland. *Angiostrongylus vasorum*, the French heartworm, was introduced to Newfoundland, presumably arriving with foxes that were imported or with infected dogs (*Canis familiaris*). Highly pathogenic in dogs, it causes clinical respiratory distress, occlusion of the pulmonary arteries, verminous pneumonia, and disseminated intravascular coagulation (Bolt et al. 1994). *Crenosoma vulpis*, the lungworm, causes severe breathing difficulties and a chronic cough in dogs (Conboy and Adams 1995). Little is known about the biology of either parasite in wild red fox populations.

The life cycle of *C. vulpis* is fairly well understood (Wetzel and Mueller 1935, Stockdale and Hulland 1975, Anderson 2000). Females are viviparous, releasing first-stage larvae (L_1) into the bronchi and bronchioles of the lung. L_1 are coughed up, swallowed, and passed in the feces where they infect terrestrial gastropod intermediate hosts. They mature to the infective, third-stage (L_3) within the foot of a slug or snail at which point they may be ingested by a fox. Wetzel and Mueller (1935) determined that once in the gastrointestinal tract, L_3 penetrate the intestinal wall and travel through the lymph vessels to the right heart, then lungs. However, Stockdale and Hulland (1975) believed that L_3 migrate through the hepatic portal system to the hepatic vein, heart, and finally lungs. The worms mature quickly and L_1 appear in feces 19-21 days after

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infection (Wetzel and Mueller 1935, Stockdale and Hulland 1975).

Adult *C. vulpis* are cream or pale yellow coloured. The males are 3.8 to 8.0 mm in length, while the females are 12.0 to 16.0 mm (Wetzel and Mueller 1935, Levine 1968, Craig and Anderson 1972, McGarry et al. 1995). Most notable perhaps is the unusual series of overlapping cuticular folds or 'crenations' at the anterior end of worms in the genus *Crenosoma* (Wetzel and Mueller 1935, Levine 1968, McGarry et al. 1995, Anderson 2000).

The host specificity of *C. vulpis* is broad, in that the parasite infects several canid species including red fox, grey fox (*Urocyon cinereoargenteus*), arctic fox (*Alopex lagopus*), wolf (*Canis lupus*), coyote (*Canis latrans*), raccoon dog (*Nyctereutes procyonoides*), European badger (*Meles meles*), and domestic dog (Skrjabin et al. 1952, Levine 1968, Stockdale and Hulland 1975, Conboy and Adams 1995, Conboy 1996, Anderson 2000, Thiess et al. 2001). It also occurs in black bear (*Ursus americanus*), brown bear (*Ursus arctos*), wolverine (*Gulo gulo*), and otter (*Lutra lutra*) (Brglez and Valentičič 1968, Anderson 1971, Addison 1978, Addison and Fraser 1994, Shimalov et al. 2000).

Crenosoma vulpis is widespread in its geographic distribution. It is present in China (Levine 1968) and throughout Europe (Dougherty 1945), including Austria (Lassnig et al.1998), the former Soviet Union (Chertkova 1962), Belarus (Shimalov et al. 2000), Hungary (Takács 2001), Germany (Wetzel and Mueller 1935, Thiess et al. 2001), Denmark (Guildal and Clausen 1973, Willingham et al. 1996), Spain (Alvarez et al. 1992), Italy (Poli et al. 1985), England (Beresford-Jones 1961) and Ireland (Reilly et al. 2000). It also occurs within eastern North America in New York State (Hanson 1933, Goble and Cook 1942, Zeh et al. 1977), Ontario (Addison 1978, Hoff 1993), New Brunswick (Smith 1978, Conboy and Adams 1995), Nova

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Scotia (Smith 1978), Prince Edward Island (Bihr and Conboy 1999) and Newfoundland (Threlfall 1969, Smith and Threlfall 1973). The extent of its distribution in Newfoundland is unknown.

Crenosoma vulpis occurs in the bronchi and bronchioles of the lungs, and rarely, the trachea (Stockdale and Hulland 1970, Zeh et al. 1977, Cobb and Fisher 1992, Conboy and Adams 1995, McGarry et al. 1995, Bihr and Conboy 1999). Clinical signs of infection include coughing, shortness of breath, reduced appetite, weakness, and emaciation (Hanson 1933, Cobb and Fisher 1992, Hoff 1993, Conboy and Adams 1995, McGarry et al. 1995, Shaw et al. 1996, Bihr and Conboy 1999, Reilly et al. 2000).

The pathology of *C. vulpis* is best known from studies of domestic dogs where infection causes pulmonary lesions, areas of emphysema, bronchitis, consolidation of the lungs, interstitial pneumonia, and blockage or thickening of the bronchioles as well as lesions in the liver from migration of infective larvae (Stockdale and Hulland 1970, Poli et al. 1985, Shaw et al. 1996). Its pathology in foxes remains virtually unstudied.

Angiostrongylus vasorum, another parasite of foxes in Newfoundland, is also heteroxenous and requires an intermediate terrestrial gastropod host to complete its life cycle. Females in the pulmonary arteries release eggs which are swept by the blood (Dorchies 1976) to the pulmonary capillaries where they hatch (Guilhon 1969, Dorchies 1976, Bourdeau 1993), releasing L_1 that migrate through the lung tissue to the alveoli (Guilhon 1969, Dodd et al. 1976, Dorchies 1976, Bourdeau 1993). From there they travel up the bronchial escalator to the mouth, are swallowed (Guilhon 1969, Dorchies 1976, Bourdeau 1993) and passed with the feces (Dorchies 1976, Bourdeau 1993). Once outside the host, the L_1 can infect a wide range of snail and slug species (Guilhon 1967, Bourdeau 1993) and mature to the infective L_3 (Bolt et al. 1994).

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At this point the gastropod is eaten by the final host and the larvae are released as the slug is digested. L_3 migrate through the wall of the duodenum (Fabian 1986) to the visceral (Anderson 2000) and mesenteric (Schelling et al. 1986) lymph nodes where they mature to the fifth stage (L_5), or subadults (Guilhon and Cens 1973, Bourdeau 1993). They use either the hepatic portal system (Schelling et al. 1986, Bourdeau 1993) or the lymphatic system (Guilhon and Cens 1973, Fabian 1986, Schelling et al. 1986) to reach the right ventricle of the heart and pulmonary arteries (Rosen et al. 1970).

Angiostrongylus vasorum males are 11.8 to 18 mm long and the females 14.9 to 25 mm (Guilhon and Cens 1973, Dorchies 1976, Lima et al. 1985, Williams et al. 1985, Perry et al. 1991, Bourdeau 1993, Bolt et al. 1994). Being hematophagous, females have a distinctive 'barber pole' appearance with the blood-filled intestine wrapped around the cream coloured ovaries (Rosen et al. 1970, Dorchies 1976, Poli et al. 1984, Bourdeau 1993, Bolt et al. 1994).

French heartworm infects a number of wild and domestic canids. It is most commonly reported in red fox (Skrjabin et al. 1952) and domestic dog (Cuillé and Darraspen 1930), but natural infections have also been found in crab-eating fox (*Cerdocyon thous*) (Lämmler et al. 1971), hoary fox (*Dusicyon vetulus*) (Lima et al. 1994), and wolves (*Canis lupus*) (Segovia et al. 2001). It has also been found in European badger (Torres et al. 1996, Torres et al. 2001) and a single domestic cat (*Felis domesticus*) (Kamenov et al. 1999). Experimental infections have been established in the jackal (*Canis aureus*) (Guilhon 1965, 1967), Nile rat (*Arvicanthis niloticus*) (Eckert and Lämmler 1972), and African desert fox (*Fennecus zerda*) (Guilhon 1965, 1967).

Angiostrongylus vasorum has a world-wide distribution. Within Europe it occurs in Ireland (Roche and Kelliher 1986), England (Jacobs and Prole 1975), Denmark (Finnerup 1983),

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France (Cuillé and Darraspen 1930), Germany and Austria (Guilhon 1969), Switzerland and Hungary (Eckert and Lämmler 1972, Ribière et al. 2001), Bulgaria (Kamenov et al. 1999), the southern countries of the former Soviet Union (Delianova 1959, Chertkova 1962), Turkey (Tigin 1972), Italy (Poli et al. 1984), Spain (Tarazona 1974, Acedo et al. 1979, Alvarez et al. 1992, Segovia et al. 2001, Torres et al. 2001), Portugal (Simpson 1996), and Greece (Diakou 1995), as well as in Asia (Skrjabin et al. 1952). It has been found in South America in Brazil (Lima et al. 1994) and Columbia (Rosen et al. 1970), and in Uganda, Africa (Bwangamoi 1972). It has also been reported from Australia (Roberts 1940). Within North America, however, it is only known to occur in Newfoundland, Canada, where it infects native red foxes and domestic dogs (Smith and Threlfall 1973, Whitney 1998, Bourque et al. 2002). There have been other reports of infection in North America, including infected dogs imported from Europe to Alberta (Perry et al. 1991) and Michigan (Williams et al. 1985), and a fennec imported from South America into Washington, D.C. (Bush and Montali 1977); however, they have all been isolated cases. A related species, *Angiocaulus gubernaculus*, originally described from badger (Dougherty 1946), has since been reported in the cardio-pulmonary circulation of the island fox (*Urocyon littoralis*) from the California Channel Islands (Faulkner et al. 2001).

Adult *A. vasorum* occur most often in pulmonary arteries, occasionally in the right ventricle of the heart (Guilhon 1963, Bwangamoi 1972, Lynch 1977, Mahaffey et al. 1981, Prestwood et al. 1981, Hubert 1985, Poli et al. 1985, Roche and Kelliher 1986, Patteson et al. 1987, Martin 1989, King et al. 1994, Simpson 1996, Costa and Tafuri 1997), and infrequently in the right auricle (Bwangamoi 1974). The majority of research has focused on the pathology of infection in dogs and comprises an extensive body of literature, primarily describing the clinical

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signs of angiostrongylosis. The most commonly reported signs of infection are coughing with mucous expectorated occasionally, dyspnoea, exercise intolerance, stunted growth, tachycardia, anaemia, and pale mucous membranes (Cuillé and Darraspen 1930, Guilhon 1963, Jacobs and Prole 1975, Guelfi 1976, Lynch 1977, Jones et al. 1980, Simpson and Neal 1982, Williams et al. 1985, Patteson et al. 1987, Martin 1989, Cobb and Fisher 1990, Koch et al. 1992, Migaud et al. 1992, Juste Jordán et al. 1993, Martin et al. 1993, Patteson et al. 1993, Ramsey et al. 1995, Cury and Lima 1996*a*, Cury and Lima 1996*b*, Simpson 1996, Cury et al. 2001, Phillips 2001). Several studies have observed bleeding tendencies (Singleton 1994) and prolonged clotting times (Dodd 1973, Caruso and Prestwood 1988), and in some cases, a condition known as disseminated intravascular coagulation (Schelling et al. 1986, Caruso and Prestwood 1988, Ramsey et al. 1995). Rarely, infected animals will display subcutaneous swelling following injury due to the blood's subsequent inability to clot (Dodd 1973, Williams et al. 1985, Cury and Lima 1996*a*). Nervous disease, lameness, and necrosis of the limb extremities have also been reported (Dodd 1973, Hubert 1985). Infected dogs occasionally show no clinical signs (Prestwood et al.1981, Juste Jordán et al. 1993).

Angiostrongylus vasorum infection causes extensive damage to the lungs and other organs. The most severely damaged areas appear dark red or brown in colour with tan or creamy yellow spots 0.25 mm to 3 cm in diameter (Cuillé and Darraspen 1930, Guilhon 1963, Mahaffey et al. 1981, Poli et al. 1984, Poli et al. 1985, Roche and Kelliher 1986, Perry et al. 1991, Poli et al.1991, Koch et al. 1992, Martin et al. 1993, Lima et al. 1994, Cury and Lima 1996*a*, Simpson 1996). The lung parenchyma feels dense and consolidated while lighter coloured nodes representing areas of interstitial pneumonia often feel firm in the middle (Cuillé and Darraspen

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1930, Mahaffey et al. 1981, Simpson and Neal 1982, Hubert 1985, Williams et al. 1985, Perry et al. 1991, Poli et al. 1991, Martin et al. 1993, King et al. 1994, Simpson 1996). Histologically, the lungs become fibrotic, edematous and emphysematous, and granulomas are formed around eggs, L_1 or adult worms (Rosen et al. 1970, Bwangamoi 1974, Mahaffey et al. 1981, Williams et al. 1985, Roche and Kelliher 1986, Poli et al. 1991, Martin et al. 1993, King et al. 1994). In severe infections the pulmonary arteries are enlarged and can be occluded either by adult worms or extensive fibrosis, which may enlarge the heart (Dodd 1973, Bwangamoi 1974, Lynch 1977, Poli et al. 1984, Martin 1989, Perry et al. 1991, Poli et al. 1991, Koch et al. 1992, Patteson et al. 1993, King et al. 1994). Fibrosis due to interstitial pneumonia in the alveolar septae can occlude the alveolar spaces (Bwangamoi 1972, Mahaffey et al. 1981, Williams et al. 1985) and the surface of the lungs may adhere to the wall of the pleural cavity (Poli et al. 1991).

The diaphragmatic lobes are more often infected than the others (Perry et al. 1991, Poli et al. 1991, Simpson 1996). Within the lobes, there appears to be a pattern of damage. Their margins are most often and most severely affected and the degree of damage decreases towards the center (Bwangamoi 1974, Dodd et al. 1976, Mahaffey et al. 1981, Prestwood et al. 1981, Roche and Kelliher 1986, Cury et al. 2001).

There are several records of aberrant larval migration (Perry et al. 1991, King et al. 1994, Reifinger and Greszl 1994), although the reports do not specify which larval stages were found in unusual locations. In normal infections, the subadults or L_5 migrate from the visceral and mesenteric lymph nodes to the pulmonary arteries via the hepatic portal or lymphatic system (Guilhon and Cens 1973, Schelling et al. 1986, Bourdeau 1993, Anderson 2000). Therefore, it is most likely that the stages which end up in sites other than the pulmonary arteries are subadult or

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L_5. Adult as well as subadult *A. vasorum* are frequently found in the eye (Perry et al. 1991, Rosenlund et al. 1993, King et al. 1994). Paralysis of the limbs (Patteson et al. 1993), nervous disease (Perry et al. 1991, Reifinger and Greszl 1994), and ruptured femoral arteries (Cury and Lima 1996*a*) have also been reported in dogs. Larvae, presumably L_5, have been located in the capillaries and sinusoids of the liver, intestine, colon, stomach, pancreas, spleen, pituitary gland, spinal cord, and brain (Perry et al. 1991, Reifinger and Greszl 1994, pers. com., Whitney). Organs such as the heart, kidney, pancreas, and lymph nodes are often distorted by severe lesions and cysts formed around migrating larvae (Bwangamoi 1974, Roche and Kelliher 1986, Costa and Tafuri 1997). Also the surface of the kidney may show pale foci and hemorrhagic lesions (Bwangamoi 1974, Perry et al. 1991, Costa and Tafuri 1997).

There were three main objectives of this study: 1.) determine the geographic distributions of *A. vasorum* and *C. vulpis* in foxes in Newfoundland, 2.) explore any relationships between the number of adult nematodes present and the number of larvae in feces, and the age, sex and health of the host, and 3.) determine if any interaction occurs between the two parasites when in the same fox.

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Materials and Methods

Collection and necropsy of carcasses

Fox carcasses were collected by staff of the Newfoundland Inland Fish and Wildlife Division of the Department of Tourism, Culture, and Recreation, and the Animal Health Division of the Department of Forest Resources and Agrifoods. Animals from 6 arbitrarily defined regions corresponding with trapper activity within Newfoundland (Fig. 1) were submitted by fur trappers during the legal trapping seasons from October 20, 2000 to February 1, 2001 and October 20, 2001 to December 31, 2001. Carcasses were frozen upon receipt and maintained at −20°C until thawed and examined 2-8 months later. A small number of coyote (*Canis latrans*) carcasses were also collected.

At necropsy, sex and body measurements including skinned weight, total length, height at right shoulder, neck circumference, head circumference, heart girth, and right hind foot length were recorded. Body condition was estimated by indexing subcutaneous body fat and by weighing omental fat. A body fat index (0-3) ranked the amount of fat present on the back of the neck, between the front and rear legs, and on the ribs. A '0' rating indicated little or no fat present, while '1' indicated a minimal amount of fat present in patches along the margins of the *latissimus dorsi* muscles, between the shoulder blades, and on the chest between the front legs. A rating of '2' was assigned when fat was present in moderate-sized patches (about 4 cm across) between the shoulder blades and/or on the chest between the front legs, a strip along the margin of the *latissimus dorsi*, and sometimes a patch on the flanks. The highest rating of '3' was given when the lower back, *latissimus dorsi* muscles, upper shoulder blades, and sternum were all well

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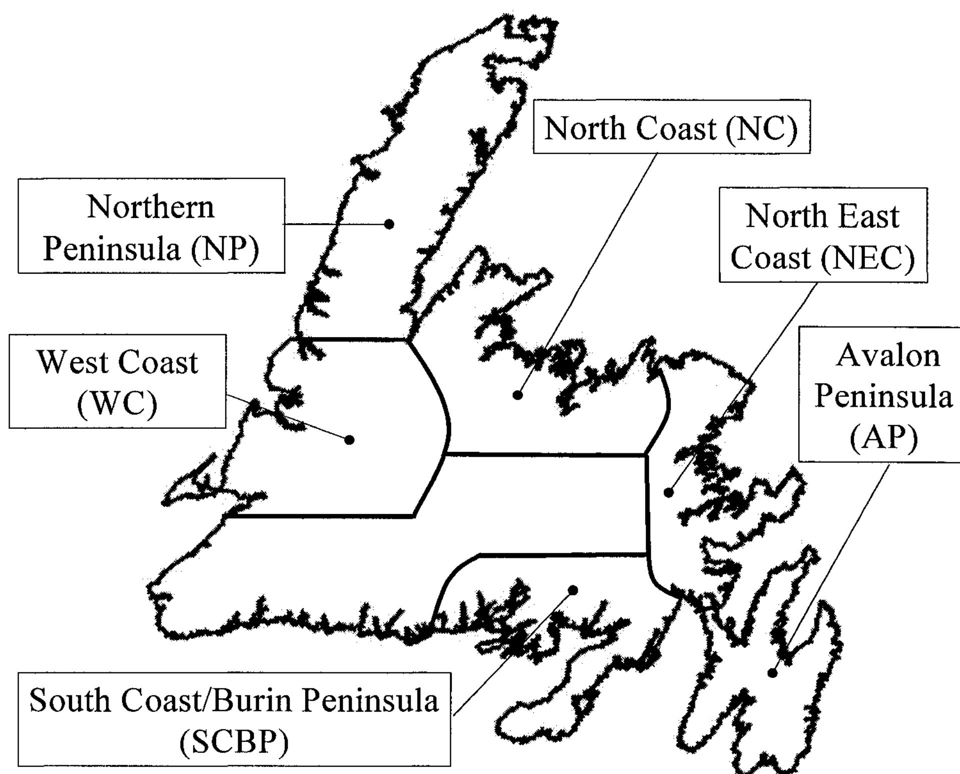

Fig 1. Map of Newfoundland showing the 6 regions where red foxes *(Vulpes vulpes)* were trapped in 2000-2001.

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covered with fat. An omental fat ratio expressing the amount of stored fat proportional to body size was calculated by dividing omental fat weight by skinned body weight. Also, the appearance and consistency of lungs on palpatation were noted. Foxes were aged by counting cementum annuli (Matson's Laboratory, LLC 2002) and for some analyses, animals were grouped into 3 age classes: young-of-the-year (YOY) (6 to 9 months), yearlings (YRLG) (1.5 to 2.5 years) and adults (3.5 years and older). Ages up to 7.5 years old were correct within +/- 0 years, and those 8.5 years and over were correct within +/- 1 years. The heart and lungs were removed together without damaging their surfaces, and refrozen in plastic bags until later thawed and examined for nematodes. Fecal samples were obtained from the distal 15 cm of the intestines which had been stored frozen in plastic bags.

Collection of nematodes from heart and lungs

In the lungs, the airways, containing *C. vulpis*, and the pulmonary arteries, containing *A. vasorum*, are closely associated. To extract both species without compromising the collection of either, a modification of a lung flush technique was used followed by dissection of the pulmonary arteries. A perfusion technique modified from Oakley (1980) was performed through the left ventricle so that a flow of water was created in the reverse direction to blood flow through the left heart, and went into the pulmonary veins rather than the arteries. To accomplish this, a small rubber hose was inserted tightly into a 5 mm incision at the base of the left ventricle and water pressure from the tap (up to approximately 3.53 kg/cm^2) was maintained by clamping the aortic arch and superior vena cava with haemostats. Water reaching the capillaries by way of the pulmonary veins broke into the alveolae, flowed into the bronchioles and bronchi, and carried *C.*

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vulpis out of the trachea. Water flowing out of the trachea was passed through a 147 μm copper sieve (Tyler Standard Screen) to collect adult worms. The heart and lungs were kept under water pressure until the lungs became a pale cream colour indicating that most of the blood had been washed out. To collect any *C. vulpis* that remained in the lungs after the flush, the airways were cut open with fine tipped scissors and any worms recovered were included with those from the lung flush. Worms were sexed on the basis of their morphology, counted, and preserved in 70% ethanol with 10% glycerin.

To examine for *A. vasorum*, each lobe of the lung was then separated from the heart by severing the main pulmonary artery and vein. Fox lungs are divided into seven lobes (Evans and deLahunta 1971); a cranial, middle, and caudal (or diaphragmatic) lobe on the left side and cranial, middle, caudal, and accessory lobes on the right. These form 4 groups of lobes based on the main branches of the pulmonary arteries (Table 1). Each lobe was dissected in a shallow bowl of water under a ring lamp and magnifying lens. The pulmonary arteries were opened by cutting along their length with finely pointed scissors down to a diameter of approximately 1 mm. Any *A. vasorum* found were removed with fine-tipped forceps, sexed on the basis of their morphology, counted and their location noted. The heart was bisected transversely through both ventricle walls, and any *A. vasorum* in the right ventricle were removed, counted, and their location noted. The heart was rinsed with water, weighed, and the thickness of the right and left ventricle walls measured at their widest points. The relative heart weight ratio (%) (heart weight/body weight) and ventricular ratio (left/right ventricle widths) were calculated as per Robinson and Maxie (1993). Occasionally, *A. vasorum* were flushed from the lungs along with *C. vulpis*, suggesting that the water pressure may have driven them from the pulmonary arteries into the bronchioles

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Table 1. Groups of lung lobes based on main branches of the pulmonary arteries.

New grouping of lung lobes	Lung lobes
Left anterior	Left cranial lobe
Left posterior	Left middle and left caudal
Right anterior	Right cranial and right middle
Right posterior	Right caudal and right accessory

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through ruptured alveolae. Although their precise origin within the lobe groups could not be determined, it was assumed that they originated from the right ventricle or from the pulmonary arteries proximal to the heart and were therefore included with those retrieved from the right ventricle. As well, *C. vulpis* were occasionally found when extracting *A. vasorum*; these were included with *C. vulpis* from the lung flush. After collection, a number of *A. vasorum* were measured and the dimensions, including total body length, body width, oesophagus, tail, spicule and gubernaculum length, excretory pore, and vulva were recorded.

Fecal analysis

Larvae were recovered from previously frozen fecal samples using a modified floatation technique. Approximately 0.3 - 0.5 g of fresh feces were macerated in 15 ml of water in a 250 ml beaker and the contents poured into a 15 ml centrifuge tube. Another 15 ml of water was used to rinse the beaker and was poured into a second tube. Both tubes were centrifuged for 3 minutes at 1240 rpm, and the supernatant pipetted off and discarded. The tubes were refilled with water and the sediment resuspended with a thin stirring rod. Any large particulate matter was allowed to settle for 10 seconds before pouring the supernatant into two separate centrifuge tubes; the settled material was discarded. The tubes were centrifuged as before, and the supernatant discarded. Concentrated sucrose solution (150.6 g sugar/100 ml water, specific gravity 1.35) was added to each tube and the settled material resuspended. The tubes were topped up with sucrose to form a positive meniscus on which a cover slip was placed and left for 2 hours before being removed and mounted on a microscope slide.

The slides were examined at 40x using a compound scope. Although *A. vasorum* L_1 are

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longer than *C. vulpis*, the difference was unclear due to distortion from the sugar solution. However, L_1 are easily distinguished on the basis of their tail morphology; *A. vasorum* has a very characteristic 'kink' in the tail plus a sub-terminal 'dorsal spine' (Rosen et al. 1970, Guilhon and Cens 1973, Bolt et al. 1994) while *C. vulpis* has a smoothly tapered tail (Craig and Anderson 1972, Cobb and Fisher 1992, McGarry et al. 1995). The first twenty L_1 on each slide were identified at 400x. A few could not be identified as they were too damaged or misshapen by the sugar solution. After twenty had been identified, the remainder of the L_1 on the slide were counted. The proportion of identified larvae was used to estimate the total numbers of *C. vulpis* and *A. vasorum*. The number of larvae recovered using the floatation technique was expressed per gram of dried fecal material.

Data analysis

Data were analysed using SPSS version 10.0 (SPSS Inc., Chicago, Illinois, USA). The normality of the data were tested with the Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf 1995). When not normally distributed ($p < 0.05$), the data were normalized with log or square root transformations (Zar 1999). The prevalence of infection between years was compared using χ^2 tests, and mean intensities were compared using Mann-Whitney U tests. If the prevalence or mean intensities did not differ between years ($p \geq 0.05$), they were combined. Among regions or ages, differences in prevalence were examined using a χ^2 followed by a Tukey-type multiple comparison test (Zar 1999), and differences in mean intensities were determined using one-way ANOVAs followed by Tukey's post-hoc multiple comparison tests. However, if the data could not be normalized by transformation, the difference in mean intensities among

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regions was evaluated using a Kruskall-Wallis test followed by the Dunn method of nonparametric multiple comparisons (Zar 1999). Three-way ANOVAs, followed by Tukey's test where necessary, were used to determine if mean adult or larval intensity differed with host sex, age and body fat index. Heart weight and ventricular ratios between *A. vasorum* positive and negative animals were compared using one-way ANOVAs. The difference in prevalence of *A. vasorum* adults between lobes of the lung and right ventricle of the heart were determined with a χ^2 test (Zar 1999). The difference in number of adults between the right ventricle and pulmonary arteries of the lungs was determined with a paired t-test while a one-way ANOVA followed by a Tukey's test was used to compare numbers of adults among lobes. Interaction between intensity of species was determined using a 2 x 2 contingency table with a G-test, and the Yates correction for continuity (Zar 1999). All significant differences were accepted at $\alpha = 0.05$.

The relationship between mean intensity of adult worms and the numbers of larvae in feces was determined using linear regression. Linear regressions were also used to examine the relationships between mean intensity and omental fat ratio, ventricular ratio, and heart weight ratio.

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Results

Skinned fox carcasses ($n = 366$) were examined from 6 different regions in Newfoundland (Fig. 1), 267 from the 2000-2001 trapping season and 99 in the following year (Table 2). Of eight coyote carcasses examined in the first year (4 from the Northern Peninsula, 1 from the North Coast, 3 from unknown locations) the prevalence of *C. vulpis* was 38% with a mean intensity of 16 ± 10.2 (4-36) (mean ± S.E. followed by range in brackets). None of the coyotes sampled were infected with *A. vasorum*.

Crenosoma vulpis

Crenosoma vulpis occurred in foxes from all 6 regions of Newfoundland (Tables 2, 3, Fig. 2). Prevalence in years 1 (86%) and 2 (89%) did not differ ($\chi^2 = 0.61$, df = 1, $p = 0.436$), and were therefore combined for an overall prevalence of 87% (Table 2, Fig. 2). Among regions, the prevalence on the Avalon Peninsula (70%) was lower than the others (91%-100%) ($\chi^2 = 30.52$, df = 5, $p < 0.001$) (Table 3).

The mean intensity of *C. vulpis* over both years was 230 ± 20.8 and one fox had as many as 3503 worms (Table 2). The mean number of adult male (106 ± 9.0) and female (133 ± 12.6) worms did not differ ($U = 43813.50$, $p = 0.275$) (Table 4). Because the intensity data were not normally distributed ($D = 0.29$, df = 366, $p < 0.001$) and could not be normalized by transformation, nonparametric methods were applied. The overall mean intensity in year 2 (290 ± 35.8) was significantly higher than in year 1 (207 ± 25.1) ($U = 8378.50$, $p = 0.020$) but differed annually by regions only on the Northern Peninsula ($U = 117.50$, $p = 0.041$), West Coast ($U =$

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Table 2. Distribution, prevalence, and mean intensity of *Crenosoma vulpis* and *Angiostrongylus vasorum* in red foxes (*Vulpes vulpes*) collected during 2000-2002 trapping seasons from 6 regions of Newfoundland.

	Crenosoma vulpis						*Angiostrongylus vasorum*					
	Prevalence (%)			Mean Intensity			Prevalence (%)			Mean Intensity		
Region	Year 1	Year 2	Total	Year 1	Year 2	Total	Year 1	Year 2	Total	Year 1	Year 2	Total
NP	86 (19/22)	95 (20/21)	91 (39/43)	43 ± 11.6 (1-195)	235 ± 85.2 (4-1272)	141 ± 46.2 (1-1272)	0 (0/22)	0 (0/21)	0 (0/43)	0	0	0
WC	89 (50/56)	100 (11/11)	91 (61/67)	165 ± 32.0 (1-899)	337 ± 81.4 (24-780)	196 ± 31.0 (1-899)	0 (0/56)	0 (0/11)	0 (0/67)	0	0	0
NC	91 (70/77)	94 (15/16)	91 (85/93)	161 ± 22.9 (1-854)	562 ± 104.9 (6-1242)	232 ± 30.9 (1-1242)	0 (0/77)	0 (0/16)	0 (0/93)	0	0	0
SCBP	100 (9/9)	100 (4/4)	100 (13/13)	73 ± 31.0 (5-277)	316 ± 151.9 (14-724)	148 ± 57.1 (5-724)	0 (0/9)	25 (1/4)	8 (1/13)	0	379 (379)	379 (379)
NEC	96 (45/47)	89 (8/9)	95 (53/56)	276 ± 76.3 (1-3352)	139 ± 57.2 (3-440)	255 ± 65.6 (1-3352)	9 (4/47)	44 (4/9)	14 (8/56)	69 ± 56.1 (2-236)	46 ± 3.0 (39-53)	58 ± 26.4 (2-236)
AP	64 (36/56)	79 (30/38)	70 (66/94)	386 ± 105.0 (1-3503)	211 ± 47.9 (1-1049)	306 ± 61.8 (1-3503)	88 (49/56)	89 (34/38)	88 (83/94)	68 ± 9.8 (1-256)	73 ± 10.7 (1-230)	70 ± 7.2 (1-256)
Total	**86 (229/267)**	**89 (88/99)**	**87 (317/366)**	**207 ± 25.1 (1-3503)**	**290 ± 35.8 (1-1272)**	**230 ± 20.8 (1-3503)**	**51 (53/103)[1]**	**76 (39/51)[1]**	**56 (92/163)[1]**	**68 ± 9.8 (1-256)**	**78 ± 12.3 (1-379)**	**72 ± 7.6 (1-379)**

Note: Northern Peninsula (NP); West Coast (WC); North Coast (NC); South Coast/Burin Peninsula (SCBP); North East Coast (NEC); and Avalon Peninsula (AP). Intensity values shown are the mean intensity ± standard error with range in brackets. Trapping season is October-February. Year 1 = Oct. 2000-Feb. 2001, year 2 = Oct. 2001-Dec. 2001.
[1] - Totals only include animals from regions where *A. vasorum* occurred.

Table 3. Differences in prevalence and mean intensity of adult *Crenosoma vulpis* in red foxes (*Vulpes vulpes*) among 6 regions of Newfoundland, 2000-2002.

Prevalence (%)	NP	WC	NC	SCBP	NEC	AP	Significance of differences among regional prevalences[1]
Total	91 (39/43)	91 (61/67)	91 (85/93)	100 (13/13)	95 (53/56)	70 (66/94)	AP NP WC NC NEC SCBP

Mean intensity	NP	WC	NC	SCBP	NEC	AP	Significance of differences among regional mean intensities[2]
Year 1	43 ± 11.6 (1-195)	165 ± 32.0 (1-899)	161 ± 22.9 (1-854)	73 ± 31.0 (5-277)	276 ± 76.3 (1-3352)	386 ± 105.0 (1-3503)	NP WC NC SCBP NEC AP
Year 2	235 ± 85.2 (4-1272)	337 ± 81.4 (24-780)	562 ± 104.9 (6-1242)	316 ± 151.9 (14-724)	139 ± 57.2 (3-440)	211 ± 47.9 (1-1049)	NEC AP NP SCBP WC NC

Note: Northern Peninsula (NP); West Coast (WC); North Coast (NC); South Coast/Burin Peninsula (SCBP); North East Coast (NEC); and Avalon Peninsula (AP). Prevalences are not shown for years separately as they are not significantly different from each other. Regions joined by line are not significantly different. Intensity values shown are the mean intensity ± standard error with range in brackets. Trapping season is October-February. Year 1 = Oct. 2000-Feb. 2001, year 2 = Oct. 2001-Dec. 2001.

[1] - Differences determined using Tukey's-type test for multiple comparison among proportions: $q_{(0.05, \infty, 6)} = 4.030$. Regions with similar *C. vulpis* prevalences share an underscore.

[2] - Differences determined using Dunn's method of nonparametric multiple comparison: $Q_{(0.05, 6)} = 2.936$. Regions with similar mean *C. vulpis* intensities share an underscore. As method is based on ranks, the order of regions by mean rank may not be the same as by mean intensity.

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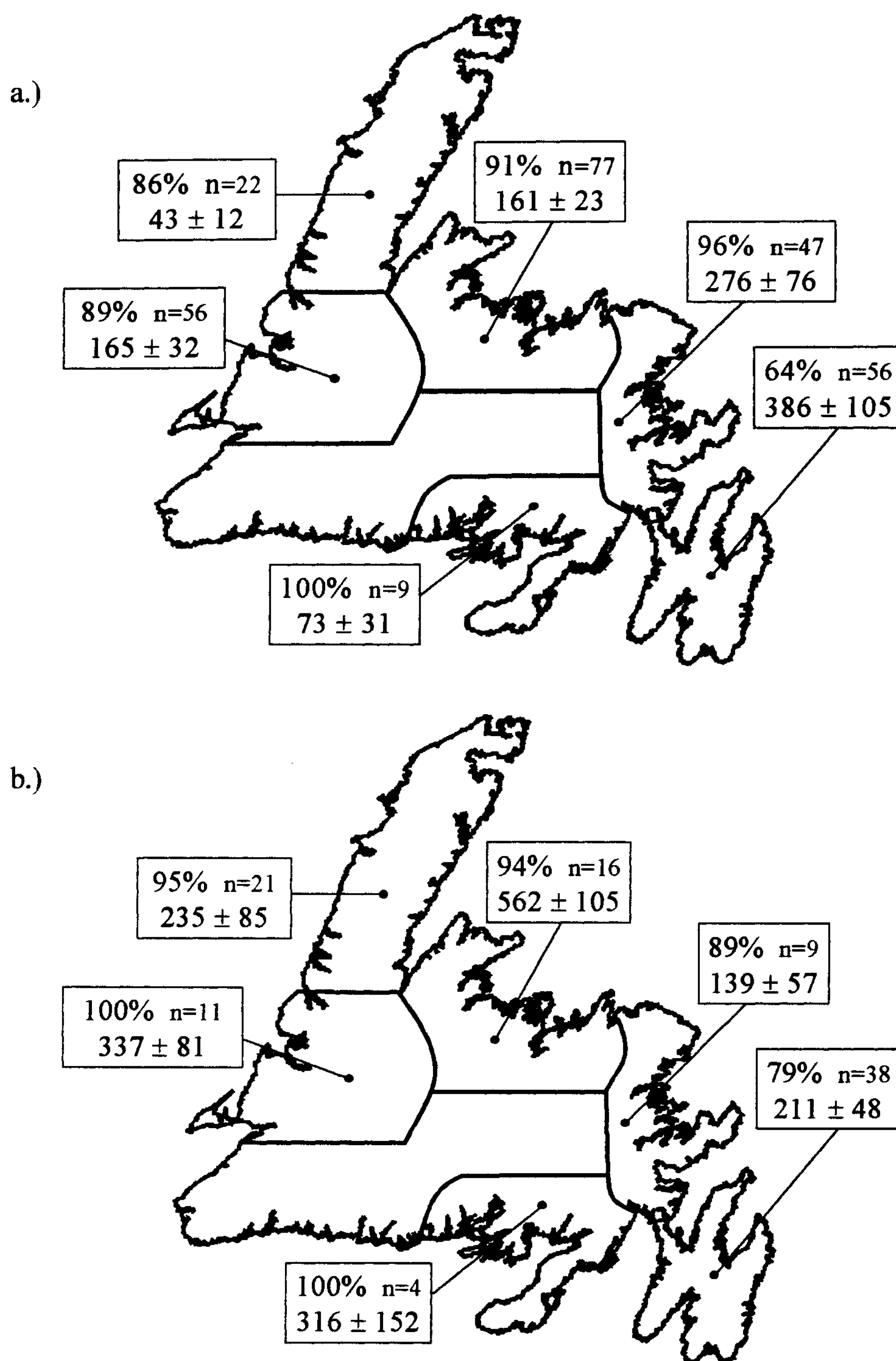

Fig. 2. Distribution, prevalence and mean intensity of *Crenosoma vulpis* in different regions of Newfoundland. a.) year 1 (Oct. 2000-Feb. 2001), b.) year 2 (Oct. 2001-Dec. 2001). Data include prevalence (%), number of animals examined (n), and mean intensity ± S.E.

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Table 4. Distribution, and mean intensity of *Crenosoma vulpis* and *Angiostrongylus vasorum* males and females in red foxes (*Vulpes vulpes*) collected in the 2000-2002 trapping seasons from 6 regions of Newfoundland.

	Crenosoma vulpis				*Angiostrongylus vasorum*			
		Mean intensity				Mean intensity		
Region	No.	# ♂	# ♀	Total	No.	# ♂	# ♀	Total
NP	39	64 ± 22.0 (1-613)	83 ± 26.2 (1-680)	141 ± 46.2 (1-1272)	0	0	0	0
WC	61	91 ± 13.7 (1-393)	110 ± 18.2 (1-522)	196 ± 31.0 (1-899)	0	0	0	0
NC	85	106 ± 14.5 (1-645)	129 ± 17.0 (1-668)	232 ± 30.9 (1-1242)	0	0	0	0
SCBP	13	65 ± 24.8 (2-309)	95 ± 36.1 (4-414)	148 ± 57.1 (5-724)	1	182 (182)	196 (196)	380 (380)
NEC	53	122 ± 26.8 (1-1165)	150 ± 42.7 (1-2187)	255 ± 65.6 (1-3352)	8	24 ± 11.7 (1-92)	35 ± 15.0 (2-135)	58 ± 26.4 (2-236)
AP	66	142 ± 27.5 (1-1364)	185 ± 38.1 (1-2139)	306 ± 61.8 (1-3503)	83	27 ± 3.0 (1-104)	43 ± 4.4 (1-161)	70 ± 7.2 (1-256)
Total	**317**	**106 ± 9.0 (1-1364)**	**133 ± 12.6 (1-2187)**	**230 ± 20.8 (1-3503)**	**92**	**28 ± 3.3 (1-182)**	**44 ± 4.5 (1-196)**	**72 ± 7.6 (1-379)**

Note: Northern Peninsula (NP), West Coast (WC), North Coast (NC), South Coast/Burin Peninsula (SCBP), North East Coast (NEC), and Avalon Peninsula (AP). Intensity values shown are the mean intensity ± standard error with range in brackets. Trapping season is October-February.

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138.0, $p = 0.010$), and North Coast ($U = 204.0$, $p < 0.001$) where intensities were higher in the second year than in the first (Table 2, Fig. 2). As the total mean intensities differed between years, they were treated separately in subsequent analyses.

In year 1, regional mean intensities differed significantly ($H = 18.71$, df = 5, $p = 0.002$) (Table 3, Fig. 2). The mean intensity on the Northern Peninsula (43 ± 11.6) was lower than on the Avalon Peninsula (386 ± 105.0) and North East Coast (276 ± 76.3). In year 2, the mean intensities among regions were different ($H = 14.62$, df = 5, $p = 0.012$); Dunn's method, however, was unable to resolve the differences (Table 3, Fig. 2).

Lungs infected only by *C. vulpis* seemed normal in texture and appearance. The surface was smooth and unblemished, and shiny red in colour, as expected in animals caught by snaring. When palpated, they were soft and spongy. Infection with *C. vulpis* was evident only by flushing with water, or dissection of the airways.

Age was determined for 288 foxes (Table 5). The oldest were 8.5 years, but most were YOY. For analysis, age classes included 175 YOY, 62 YRLG, and 51 adults. Although prevalence differed among age classes ($\chi^2 = 34.78$, df = 2, $p < 0.001$) with YOY having a higher prevalence (96%) than YRLG (73%) and adults (71%) ($q_{(0.05, \infty, 3)} = 3.314$), it did not differ between sexes ($\chi^2 = 1.44$, df = 1, $p = 0.23$). A three-way ANOVA was performed on data from year 1 only as data from year 2 could not be normalized. The model was significant ($F_{[21, 153]} = 2.48$, $p = 0.001$), and determined that of host age, sex, and body fat index, mean *C. vulpis* intensity was related to age only ($F_{[2, 153]} = 11.07$, $p < 0.001$) (Tables 6, 7). Tukey's test determined that although mean intensities in YRLG (91 ± 31.2) and adults (78 ± 41.1) were not different from each other, they were lower than in YOY (260 ± 39.4) (Table 6). Non-parametric

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Table 5. Body measurements of red foxes (*Vulpes vulpes*) collected in the 2000-2002 trapping seasons from Newfoundland.

	Number examined									Measurements								
				Location														
Age class[1]	Total [2]	♂	♀	NP	WC	NC	SCBP	NEC	AP	Skinned weight (kg)	Shoulder height (cm)	Body length (cm)	Neck circ. (cm)	Heart girth (cm)	Head circ. (cm)	Right hind foot length (cm)	Body fat index[3]	Omental fat (g)
YOY	175	93	75	23	32	43	5	27	45	5.0 ± 0.07 (2.8-7.3)	39.6 ± 0.18 (29.0-48.8)	103.4 ± 0.39 (86.2-114.6)	16.7 ± 0.20 (7.5-28.6)	28.8 ± 0.20 (17.3-38.8)	23.0 ± 0.14 (13.7-27.3)	15.6 ± 0.10 (13.4-28.4)	1.1 ± 0.07 (0-3)	42.3 ± 1.92 (0.0-132.1)
YRLG	62	33	27	10	17	7	3	3	22	5.6 ± 0.12 (3.5-8.7)	39.8 ± 0.32 (27.7-44.1)	102.8 ± 0.70 (92.0-15.5)	17.9 ± 0.24 (14.5-28.8)	29.7 ± 0.27 (23.8-35.0)	24.1 ± 0.18 (21.5-27.6)	15.7 ± 0.09 (14.5-17.5)	1.1 ± 0.12 (0-3)	46.4 ± 3.90 (7.7-146.6)
Adult	51	28	22	7	10	6	2	12	14	5.6 ± 0.14 (4.0-8.0)	40.0 ± 0.27 (36.9-43.4)	103.2 ± 0.94 (78.0-118.1)	18.0 ± 0.33 (14.5-28.8)	29.6 ± 0.40 (18.3-35.0)	24.1 ± 0.18 (21.9-27.1)	15.5 ± 0.10 (14.0-16.8)	1.3 ± 0.13 (0-3)	55.2 ± 4.77 (5.7-169.3)
Total	**288**	**154**	**124**	**40**	**59**	**56**	**10**	**42**	**81**	**5.1 ± 0.05 (2.5-8.7)**	**39.6 ± 0.14 (23.40-48.80)**	**103.1 ± 0.28 (78.0-118.1)**	**17.2 ± 0.12 (7.5-28.8)**	**29.0 ± 0.14 (16.8-38.8)**	**23.4 ± 0.09 (13.7-29.2)**	**15.6 ± 0.05 (13.4-28.4)**	**1.1 ± 0.05 (0-3)**	**43.5 ± 1.45 (0-169.3)**

Note: Northern Peninsula (NP); West Coast (WC); North Coast (NC); South Coast/Burin Peninsula (SCBP); North East Coast (NEC); Avalon Peninsula (AP); young-of-the-year (YOY); yearling (YRLG); circumference (circ.). Values shown are the mean measurement ± standard error with range in brackets. Trapping season is October-February.

[1] - Aged by cementum ring counts. Young-of-the-year = 6-9 months, yearling = 1.5-2.5 years, and adult = 3.5-8.5 years.

[2] - Totals are greater than the combined number of males and females as it was not possible to determine the sex of 10 foxes.

[3] - Body fat rated on 0-3 index, with 0 indicating little to no fat, and 3 indicating a thick layer of fat on the sides and back of the animal.

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Table 6. Prevalence and mean intensity of *Crenosoma vulpis* and *Angiostrongylus vasorum* in 3 age classes of red foxes (*Vulpes vulpes*) collected during 2000-2002 trapping seasons.

	Crenosoma vulpis						*Angiostrongylus vasorum*					
	Prevalence (%)			Mean intensity			Prevalence (%)			Mean intensity		
Age Class[1]	Year 1	Year 2	Total	Year 1	Year 2	Total	Year 1	Year 2	Total	Year 1	Year 2	Total
YOY	96 (104/108)	96 (64/67)	96 (168/175)	260 ± 39.4 (1-3352)	383 ± 43.7 (4-1272)	307 ± 29.8 (1-3352)	45 (20/44)	66 (22/33)	24 (42/77)	55 ± 11.2 (1-174)	81 ± 14.8 (1-230)	69 ± 9.5 (1-230)
YRLG	74 (35/47)	67 (10/15)	73 (45/62)	91 ± 31.2 (1-1013)	34 ± 14.4 (1-123)	79 ± 24.7 (1-1013)	70 (14/20)	88 (7/8)	34 (21/28)	99 ± 22.3 (4-229)	63 ± 21.7 (13-187)	87 ± 16.6 (4-229)
Adult	66 (23/35)	81 (13/16)	71 (36/51)	78 ± 41.1 (2-899)	52 ± 26.3 (1-344)	69 ± 27.7 (1-899)	42 (8/19)	100 (9/9)	33 (17/28)	67 ± 30.0 (2-236)	84 ± 37.3 (15-379)	76 ± 23.7 (2-379)
Total	**86 (229/267)**	**89 (87/98)**	**86 (317/367)**	**198 ± 27.5 (1-3352)**	**293 ± 36.1 (1-1272)**	**230 ± 20.8 (1-3503)**	**51 (42/83)**[2]	**76 (38/50)**[2]	**60 (80/133)**[2]	**72 ± 10.9 (1-236)**	**79 ± 12.6 (1-379)**	**75 ± 8.2 (1-379)**

Note: Young-of-the-year (YOY); yearling (YRLG). Intensity values shown are the mean intensity ± standard error with range in brackets. Trapping season is October-February. Year 1 = Oct. 2000-Feb. 2001, year 2 = Oct. 2001-Dec. 2001.

[1] - Aged by cementum ring counts. Young-of-the-year = 6-9 months, yearling = 1.5-2.5 years, and adult 3.5-8.5 years.

[2] - Totals only include animals from regions where *A. vasorum* occurred.

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Table 7. Results of three-way ANOVAs comparing mean intensities of *Crenosoma vulpis* and *Angiostrongylus vasorum* adults and larvae and sex, age class and body fat index. Collected from red foxes (*Vulpes vulpes*) during 2000-2002 trapping seasons.

	Crenosoma vulpis								*Angiostrongylus vasorum*							
	Adults[2]				Larvae[3]				Adults[3]				Larvae[3]			
Source of variation	Sum of Squares	df	*F*	*p*	Sum of Squares	df	*F*	*p*	Sum of Squares	df	*F*	*p*	Sum of Squares	df	*F*	*p*
Corrected model	144.58	21	2.48	**0.001**	156.97	21	3.30	**< 0.001**	508.65	21	1.45	0.140	10.76	13	0.89	0.597
Intercept	600.76	1	216.38	< 0.001	604.82	1	267.21	< 0.001	2085.21	1	124.89	< 0.001	116.74	1	125.98	< 0.001
Sex	4.55	1	1.64	0.203	1.63	1	0.72	0.398	3.86	1	0.23	0.633	0.09	1	0.09	0.772
Age class[1]	61.47	2	11.07	**< 0.001**	85.95	2	18.99	**< 0.001**	22.71	2	0.68	0.511	4.54	2	2.45	0.167
Body fat index	10.95	3	1.31	0.272	6.81	3	1.00	0.395	54.67	3	1.09	0.361	0.78	3	0.28	0.838
Sex x age class	5.61	2	1.01	0.367	2.96	2	0.66	0.522	61.18	2	1.83	0.170	0.29	2	0.16	0.860
Sex x body fat index	18.75	3	2.25	0.085	4.83	3	0.71	0.548	120.15	3	2.40	0.079	0.08	1	0.09	0.773
Age class x body fat index	8.96	6	0.54	0.779	3.97	6	0.29	0.939	17.85	6	0.18	0.982	0.84	2	0.46	0.655
Sex x age class x body fat index	20.80	4	1.87	0.119	3.40	4	0.38	0.826	53.59	4	0.80	0.529	0.00	0	—	—
Adjusted R^2	0.168				0.274				0.116				-0.079			

Note: Trapping season is October-February. Year 1 = Oct. 2000-Feb. 2001, year 2 = Oct. 2001-Dec. 2001.
[1] - Aged by cementum ring counts.
[2] - Year 1 only as data from year 2 data could not be normalized.
[3] - Years combined.

analysis of year 2 found that the mean intensity in YOY (383 ± 43.7) was also higher than in YRLG (34 ± 14.4) and adults (52 ± 26.3) ($Q_{(0.05, 3)} = 2.394$) (Table 6). There was a significant negative linear relationship between intensity and omental fat ratio (ln(*C. vulpis* intensity) = −0.063(omental fat ratio) + 4.620, adjusted $r^2 = 0.017$, $F_{[1, 222]} = 4.78$, $p = 0.030$), but it was extremely weak explaining only 1.7% of the variation in the data.

The relationships between *C. vulpis* L_1 output and other factors were also explored. *Crenosoma vulpis* larval output from both years increased with the number of adult worms (ln(number *C. vulpis* larvae/g dry feces) = 0.416[ln(*C. vulpis* intensity)] + 2.216, adjusted $r^2 = 0.199$, $F_{[1, 135]} = 34.84$, $p < 0.001$) (Fig. 3). Mean larval output was related to host age (model: $F_{[21, 127]} = 3.30$, $p < 0.001$; age: $F_{[2, 127]} = 18.99$, $p < 0.001$) and not to sex, or body fat index (Tables 7, 8). Tukey's test determined that YOY had a higher *C. vulpis* larval output (348 ± 88.3) than YRLG (141 ± 99.5) or adults (45 ± 14.8) (Table 8). There was a slight decrease in omental fat ratio with increasing *C. vulpis* larval output (ln(number *C. vulpis* larvae/g dry feces) = −0.060(omental fat ratio) + 4.613, adjusted $r^2 = 0.021$, $F_{[1, 139]} = 3.99$, $p = 0.048$); the relationship, however, explained only 2.1% of the variation in the data.

Angiostrongylus vasorum

Twenty males and 9 females were measured (Table 9), and dimensions corresponded with published values for *Angiostrongylus vasorum* (Rosen et al. 1970, Guilhon and Cens 1973). *Angiostrongylus vasorum* occurred in only 3 regions of Newfoundland: the Avalon Peninsula, North East Coast, and South Coast/Burin Peninsula (Table 2, Fig. 4). Figure 5 shows the distribution of *A. vasorum* positive foxes in relation to average winter thermoclines (December to

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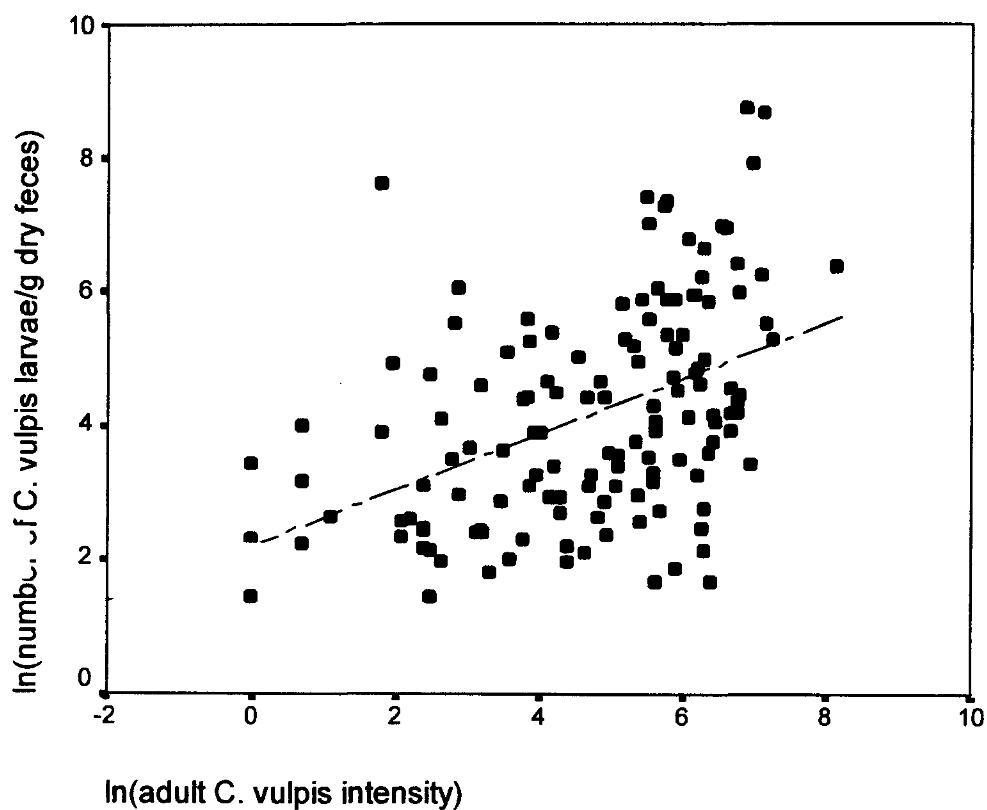

Fig. 3. Regression of adult *C. vulpis* intensity vs larval output (ln(number of *C. vulpis* larvae/g dry feces) = 0.416[ln(adult *C. vulpis* intensity)] + 2.216, adjusted $r^2 = 0.199$, $F_{[1,135]} = 34.844$, $p < 0.001$).

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Table 8. Prevalence and mean number of *Crenosoma vulpis* and *Angiostrongylus vasorum* larvae in 3 age classes of red foxes (*Vulpes vulpes*) collected during 2000-2002 trapping seasons.

	Crenosoma vulpis						*Angiostrongylus vasorum*					
	Prevalence (%)			Mean number larvae/gm dry feces			Prevalence (%)			Mean number larvae/gm dry feces		
Age Class[1]	Year 1	Year 2	Total	Year 1	Year 2	Total	Year 1	Year 2	Total	Year 1	Year 2	Total
YOY	61 (64/105)	70 (40/57)	64 (104/162)	270 ± 101.1 (6-6279)	472 ± 162.9 (4-5821)	348 ± 88.3 (4-6279)	7 (3/42)	14 (4/28)	10 (7/70)	12 ± 2.3 (8-15)	24 ± 10.0 (5-51)	18 ± 5.3 (5-51)
YRLG	39 (16/41)	33 (4/12)	38 (20/53)	170 ± 124.0 (6-2011)	24 ± 9.6 (7-50)	141 ± 99.5 (6-2011)	13 (2/16)	40 (2/5)	19 (4/21)	92 ± 44.2 (48-136)	13 ± 1.1 (11-14)	52 ± 29.2 (11-136)
Adult	47 (14/30)	36 (5/14)	43 (19/44)	45 ± 18.5 (4-258)	45 ± 24.5 (7-141)	45 ± 14.8 (4-258)	36 (5/14)	38 (3/8)	36 (8/22)	50 ± 17.4 (15-103)	41 ± 12.4 (23-65)	47 ± 11.3 (15-103)
Total	**55 (94/176)**	**59 (49/83)**	**55 (145/265)**	**219 ± 72.2 (4-6279)**	**372 ± 134.9 (4-5821)**	**276 ± 65.5 (4-6279)**	**14 (10/72)**	**22 (9/41)**	**17 (19/113)**	**47 ± 14.1 (8-137)**	**27 ± 6.6 (5-65)**	**36 ± 7.9 (4-136)**

Note: Young-of-the-year (YOY); yearling (YRLG). Larval values shown are the mean number larvae/gram dry feces ± standard error with range in brackets. Trapping season is October-February. Year 1 = Oct. 2000-Feb. 2001, year 2 = Oct. 2001-Dec. 2001.

[1] - Aged by cementum ring counts. Young-of-the-year = 6-9 months, yearling = 1.5-2.5 years, and adult = 3.5-8.5 years.

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Table 9. Comparison of body measurements of *Angiostrongylus vasorum*, *Angiocaulus gubernaculatus*, and *Angiostrongylus raillieti*.

	Angiostrongylus vasorum			*Angiocaulus gubernaculatus*		*Angiostrongylus raillieti*
	From Newfoundland, 2000-2002	Rosen et al. 1970	Guilhon and Cens 1973	Dougherty 1946	Faulkner et al. 2001	Travassos 1927
Host	Red fox	Dog	Dog	Badger	Island fox	Crab-eating fox
Males						
Number	20	10	—	4	2 (1 whole, 1 tail)	—
Length (mm)	13.5 ± 0.26 (11.5-16.0)	14.8 (13.7-15.0)	15 (14-15.5)	(18-19.5)	11.9	(13-15)
Width	219 ± 4.2 (190-255)	230 (200-240)	200 (170-235)	300 max.	240	(210-220)
Oesophagus	245 ± 5.8 (202-302)	250 (230-270)	250 (220-275)	(300-335)	—	(260-310)
Nerve ring	—	180 (160-200)	(80-92)	—	—	(190-250)
Excretory pore	416 ± 12.6 (320-541)	300 (720-320)	330 (310-350)	—	—	(340-440)
Spicule length	451 ± 12.8 (270-551) (right) 457 ± 11.8 (300-525) (left)	460 (440-490)	450 (400-480) (right) 480 (450-500) (left)	(520-560)	(500-520)	(418-494)
Gubernaculum	42 ± 1.2 (32-55)	absent	46 (40-55)	(45-50)	(34-40)	absent
Females						
Number	9	10	—	4	4 (1 whole, 3 tails)	—
Length (mm)	17.8 ± 0.8 (15.0-22.5)	19.9 (18.6-21.3)	18 (15-20.5)	(22.0-24.0)	23	(15-20)
Width	291 ± 9.1 (245-327)	300 (290-310)	270 (220-306)	350 max.	296	(230-280)
Oesophagus	273 ± 8.9 (245-326)	270 (210-300)	265 (240-280)	(335-350)	308	(260-310)
Nerve ring	—	220 (200-240)	(80-96)	—	—	(190-250)
Excretory pore	470 ± 21.4 (366-560)	420 (380-460)	355 (350-370)	—	—	(340-440)
Vulva	487 ± 115.4 (234-1157)	—	260 (220-315)	(205-250)[1]	(208-288)	210
Tail	83 ± 9.8 (62-158)	75 (61-88)	78 (67-100)	(75-90)	—	(68-83)

Note: Measurements, in μm unless otherwise stated, expressed as the mean value ± standard error with range in brackets. Oesophagus = length of oesophagus; gubernaculum = length of gubernaculum; nerve ring = distance from anterior end to nerve ring; excretory pore = distance from anterior end to excretory pore; vulva = distance from vulva to posterior end; tail = distance from anus to posterior end.
[1] = distance between vulva and anus

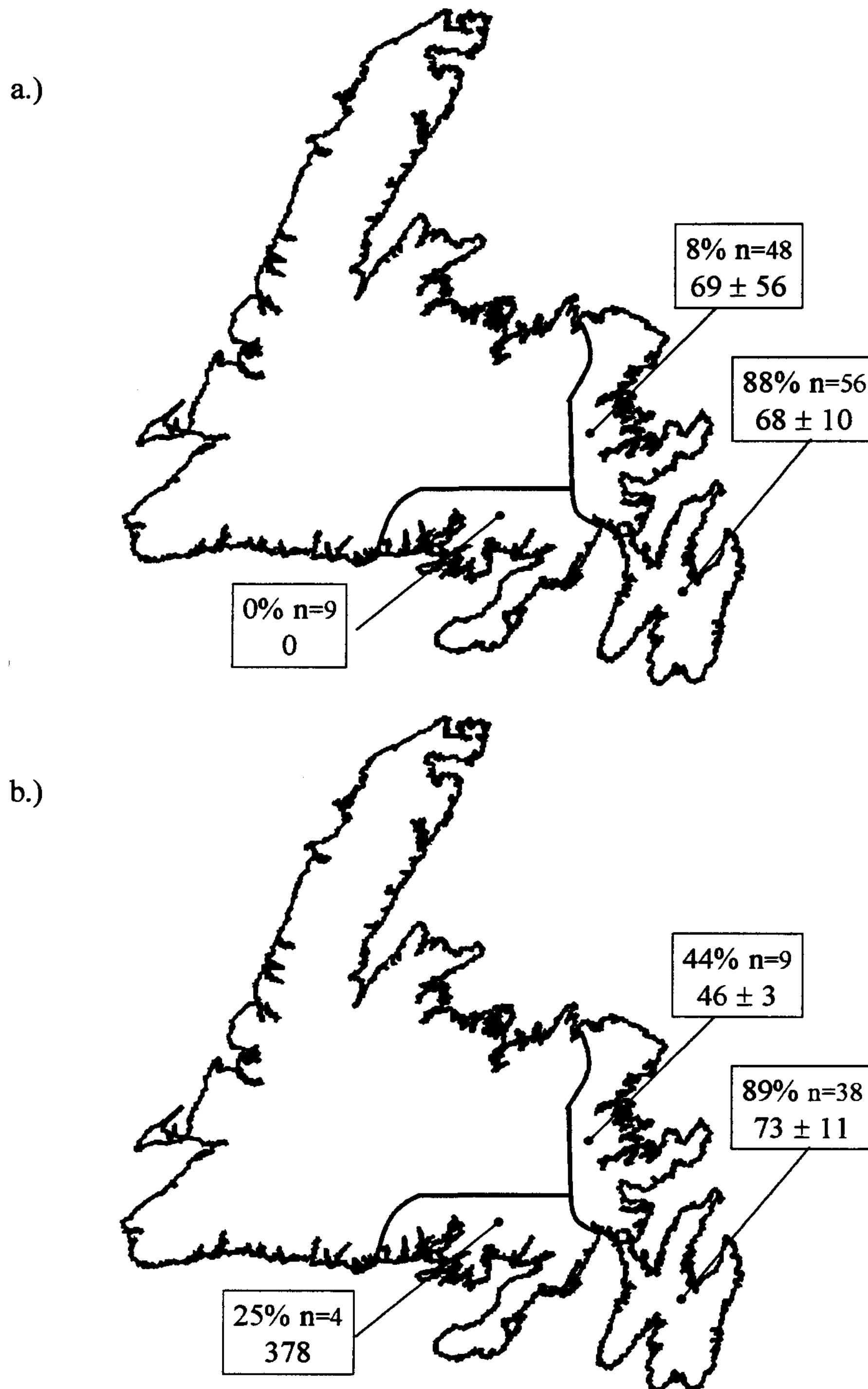

Fig. 4. Distribution, prevalence and mean intensity of *Angiostrongylus vasorum* in different regions of Newfoundland. a.) year 1 (Oct. 2000-Feb. 2001), b.) year 2 (Oct. 2001-Dec. 2001). Data include prevalence (%), number of animals examined (n), and mean intensity ± S.E.

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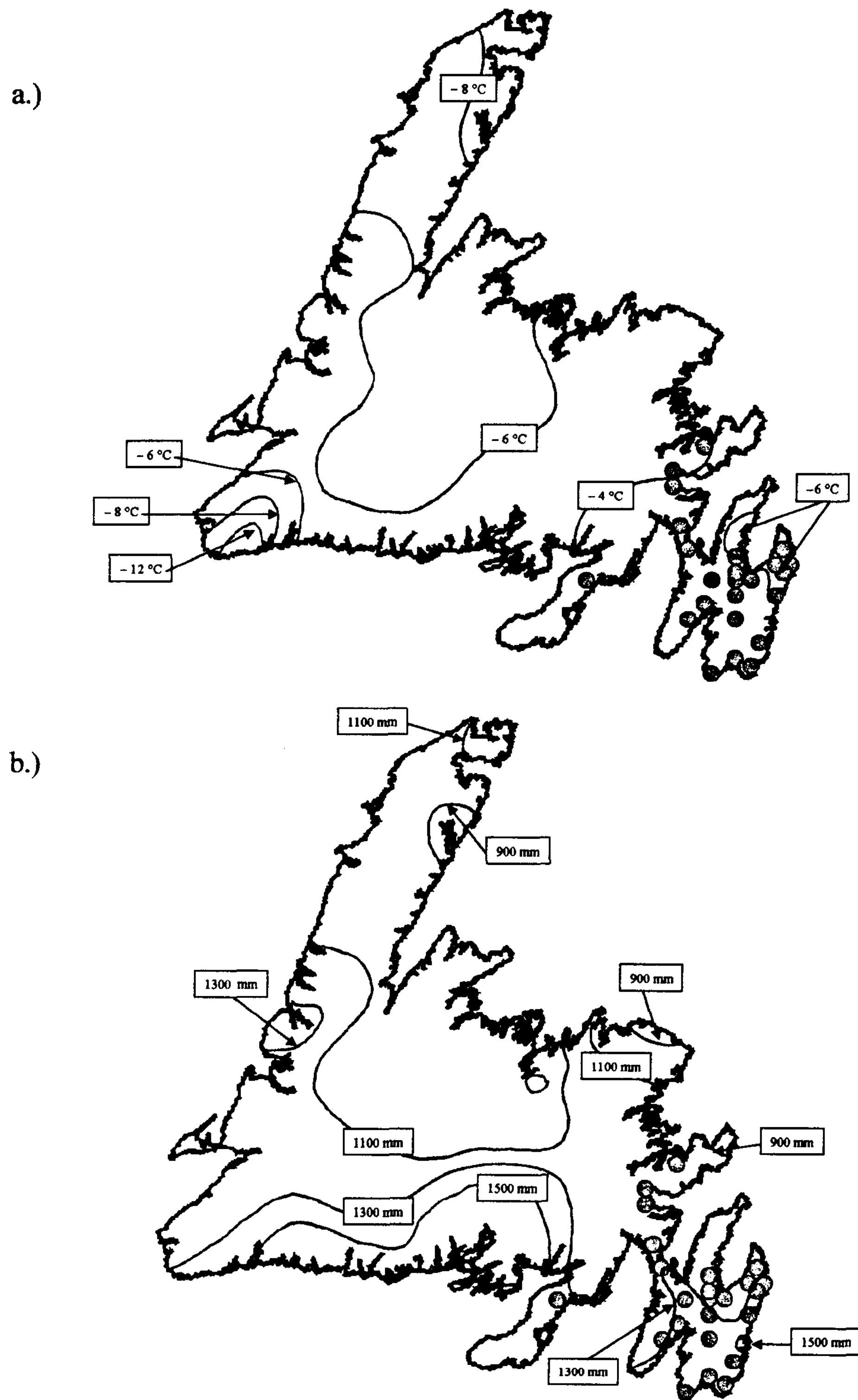

Fig. 5. Distribution of *Angiostrongylus vasorum* in Newfoundland. a.) Mean winter thermoclines (December-February) (°C). b.) Mean annual precipitation (mm). (from Water Resources Atlas of Newfoundland 1992). Dots indicate locations of *A. vasorum* infected fox.

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February) and mean annual precipitation data. The overall prevalence in areas where *A. vasorum* occurred was 56%. The prevalence in year 1 (51%) was lower than in year 2 (76%) ($\chi^2 = 12.47$, df = 1, $p < 0.001$), therefore years were considered separately. In year 1, *A. vasorum* was found on the Avalon Peninsula (88%) as well as on the North East Coast (9%) (Tables 2, 10, Fig. 4). In year 2, it was found not only on the Avalon Peninsula (89%) and the North East Coast (44%), but was also discovered in the South Coast/Burin Peninsula region (25%) (Table 2, Fig. 4). The prevalence on the Avalon Peninsula was higher than on the South Coast/Burin Peninsula and North East Coast (Table 10).

The overall mean *A. vasorum* intensity was 72 ± 7.6 (Table 2, Fig. 4) and square root transformed data from both years indicated that foxes on the Avalon Peninsula (70 ± 7.2) had a higher mean intensity than those on the North East Coast (58 ± 26.4) ($F_{[2, 90]} = 4.61$, $p = 0.012$). Despite having such a high intensity (378), the South Coast/Burin Peninsula was not included in the Tukey's test as there was only one *A. vasorum* positive fox from this region (Table 2). In foxes infected with *A. vasorum*, there were more female worms (44 ± 4.5) retrieved from the lungs than males (28 ± 3.3) ($F_{[1, 174]} = 6.72$, $p = 0.010$) (Table 4).

Lungs with *A. vasorum* were easily recognized. The diaphragmatic lobes were most often affected and distal margins were more frequently and more severely damaged than the rest of the lobe. The surface of the affected areas was often mottled and yellow-grey in appearance. Lungs were consolidated and rubbery, and felt much heavier and denser than healthy lungs. The most heavily damaged lungs had distinct firm nodes which frequently contained adult *A. vasorum*. Occasionally, there were hard, calcareous yellow deposits associated with the heavily damaged areas.

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Table 10. Differences in adult *Angiostrongylus vasorum* prevalence among 6 regions of Newfoundland. Collected from red foxes (*Vulpes vulpes*) during 2000-2002 trapping seasons.

Prevalence (%)	NP	WC	NC	SCBP	NEC	AP	Significance of differences among regional prevalences[1]
Year 1	0 (0/22)	0 (0/56)	0 (0/77)	0 (0/9)	9 (4/47)	88 (49/56)	NEC AP[2]
Year 2	0 (0/21)	0 (0/11)	0 (0/16)	25 (1/4)	44 (4/9)	89 (34/38)	SCBP NEC AP[3]

Note: Northern Peninsula (NP); West Coast (WC); North Coast (NC); South Coast/Burin Peninsula (SCBP); North East Coast (NEC); and Avalon Peninsula (AP). Years are shown separately as they are significantly different. Trapping season is October-February. Year 1 = Oct. 2000-Feb. 2001, year 2 = Oct. 2001-Dec. 2001.

1 - Only regions where *A. vasorum* occurs were compared.

2 - Difference determined using χ^2 - test: $\chi^2 = 64.819$, df=1, $p < 0.001$

3 - Differences determined using Tukey's-type test for multiple comparison among proportions: $q_{(0.05, \infty, 3)} = 3.314$. Regions with similar *A. vasorum* prevalences share an underscore.

Of fox infected with *A. vasorum*, more animals had adult worms in the pulmonary arteries (95%) than in the right ventricle of the heart (78%) ($\chi^2 = 10.42$, df = 1, $p = 0.001$) (Table 11). There were also more animals with adult worms in both the right ventricle and pulmonary arteries (73%) than in just the pulmonary arteries (22%) or in the right ventricle only (5%) ($\chi^2 = 102.36$, df = 2, $p < 0.001$). A paired t-test found that there were more *A. vasorum* in the pulmonary arteries (75 ± 8.7) than the right ventricle (10 ± 1.9) ($t_{[67]} = -7.57$, p < 0.001) (Table 12). The prevalence of worms among the four lung lobe groups did not differ ($\chi^2 = 3.37$, df = 3, $p =$ 0.338), but the number of worms among the lobe groups did. The number of worms did not differ between right (39 ± 4.2) and left (32 ± 3.8) lobe groups ($F_{[1, 164]} = 1.70$, $p = 0.194$), but the posterior lobes (47 ± 5.4) had more *A. vasorum* than the anterior (24 ± 2.5) ($F_{[1, 161]} = 13.39$, $p <$ 0.001).

Mean heart weight ratio (%) was 0.91 ± 0.011 (0.39-1.56) and the mean ventricular ratio was 4.03 ± 0.157 (0.37-36.25). Foxes with *A. vasorum* infections had a lower mean heart weight ratio (0.87 ± 0.020) than uninfected animals (0.93 ± 0.013) ($F_{[1, 268]} = 5.19$, $p = 0.023$) (Table 13). There was no significant relationship between heart weight ratio and number of *A. vasorum* adults (ln(heart weight ratio) = $-0.003\sqrt{A.\ vasorum \text{ intensity} + 0.5} - 0.133$, adjusted $r^2 = -0.009$, $F_{[1, 71]}$ = 5.19, $p = 0.568$) (Fig. 6a). Ventricular ratios did not differ between *A. vasorum* infected (4.06 ± 0.284) and uninfected animals (4.02 ± 0.188) ($F_{[1, 268]} = 0.12$, $p = 0.914$) (Table 13). Also, there was no relationship between intensity and ventricular ratio (ln(ventricular ratio) = $-0.009\sqrt{A.\ vasorum \text{ intensity} + 0.5} + 1.373$, adjusted $r^2 = 0.005$, $F_{[1, 54]} = 1.26$, $p = 0.267$) (Fig. 6b).

The prevalence of *A. vasorum* did not differ among ages in either year (year 1: $\chi^2 = 4.03$

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Table 11. Prevalence of *Angiostrongylus vasorum* in pulmonary arteries and right ventricle of red foxes (*Vulpes vulpes*) collected from Newfoundland during the 2000-2002 trapping seasons.

Location of *Angiostrongylus vasorum*	Prevalence[1] (%)
Right ventricle	78 (72/92)
Pulmonary arteries of lungs	95 (87/92)
Right ventricle only	5 (5/92)
Pulmonary arteries of lungs only	22 (20/92)
Right ventricle and pulmonary arteries of lungs	73 (67/92)

Note: Trapping season is October-February.
[1] - Only includes animals infected with *A. vasorum.*

Table 12. Mean intensity of *Angiostrongylus vasorum* in pulmonary arteries and right ventricle of red foxes (*Vulpes vulpes*) collected from Newfoundland during the 2000-2002 trapping seasons.

	Proportion with *A. vasorum* (%)[1]	Mean intensity
Lung lobe groups		
All lobes combined	95 (87/92)	75 ± 8.7 (1-375)
Anterior lobes combined	84 (77/92)	24 ± 2.5 (1-96)
Posterior lobes combined	93 (86/92)	47 ± 5.4 (1-302)
Left lobes combined	72 (66/92)	32 ± 3.8 (1-186)
Right lobes combined	79 (73/92)	39 ± 4.2 (1-189)
Right ventricle of the heart	78 (72/92)	10 ± 1.9 (1-105)

Note: Intensity values shown are the mean intensity ± standard error with range in brackets. Trapping season is October-February.
[1] - Only includes animals infected with *A. vasorum.*

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Table 13. Mean heart weight and ventricular ratios in red foxes (*Vulpes vulpes*) with and without *Angiostrongylus vasorum* in Newfoundland during the 2000-2002 trapping seasons.

Infection Status	Number of Foxes	Mean heart weight ratio (%)	Mean ventricular ratio
Uninfected	197	0.93 ± 0.013 (0.6-1.56)	4.02 ± 0.188 (0.37-36.25)
A. vasorum present	73	0.87 ± 0.020 (0.39-1.24)	4.06 ± 0.284 (1.71-21.50)

Note: Values shown are the mean ± standard error; the ranges are in brackets. Mean heart weight ratio = (heart weight (kg)/skinned body weight (kg)) x 100; mean ventricular ratio = left ventricle wall width (mm)/right ventricle wall width (mm). Trapping season is October-February.

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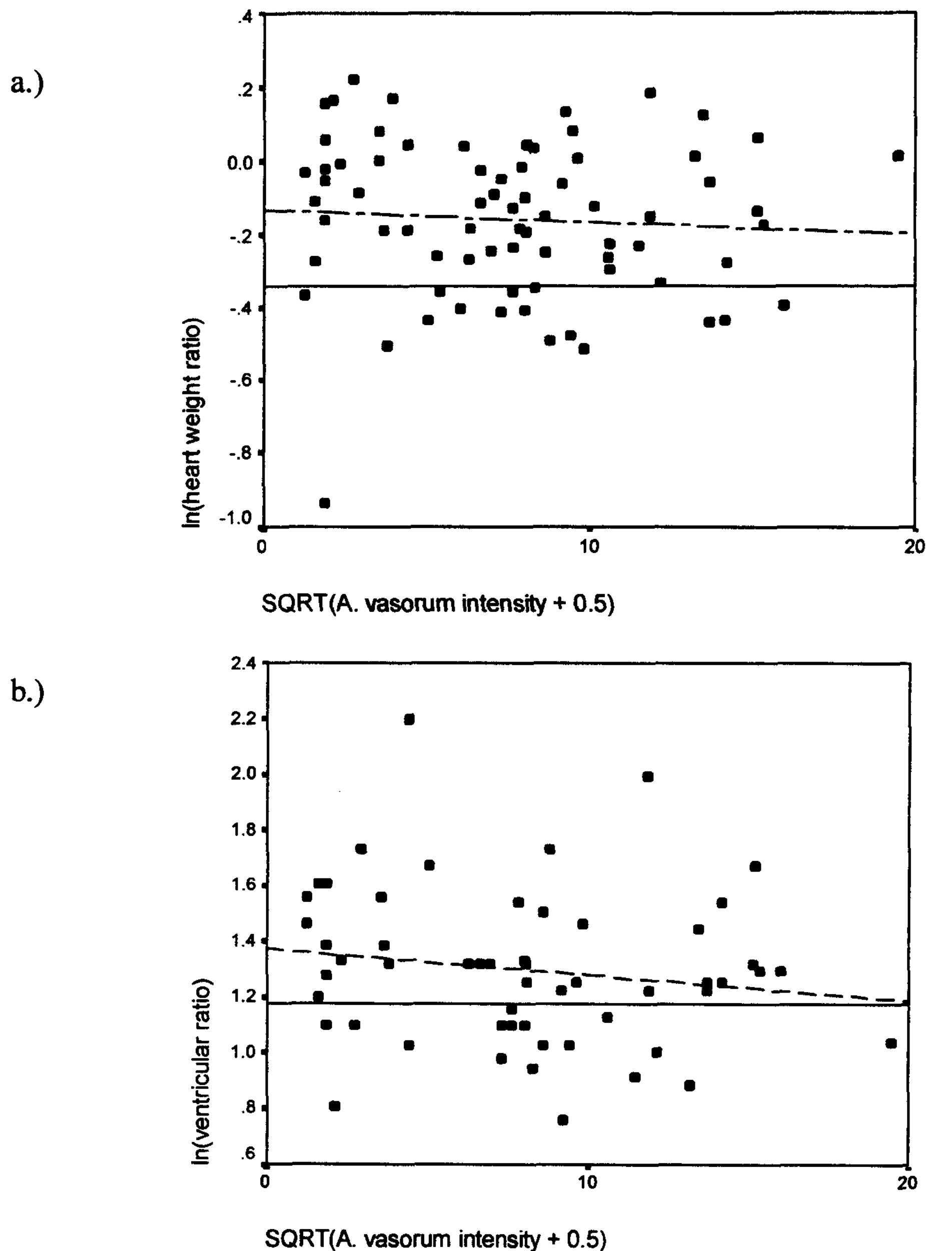

Fig. 6. Regression of *Angiostrongylus vasorum* intensity with:
a.) heart weight ratio: ln(heart weight ratio) = $-0.003\sqrt{A.\ vasorum\ \text{intensity} + 0.5}$ -0.133, adjusted $r^2 = -0.009$, $F_{[1,71]} = 0.328$, $p = 0.568$.
– – – = ln(heart/body weight ratio) based on regression equation,
—— = ln(heart/body weight ratio) in healthy dogs. (from Robinson and Maxie 1993)

b.) ventricular ratio: ln(ventricular ratio) = $-0.009\sqrt{A.\ vasorum\ \text{intensity} + 0.5}$ $+ 1.373$, adjusted $r^2 = 0.005$, $F_{[1,53]} = 1.258$, $p = 0.276$.
– – – = ln(left/right ventricle width ratio) based on regression equation,
—— = ln(average left/right ventricle ratio) in healthy dogs. (from Robinson and Maxie 1993)

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df = 2, p = 1.34; year 2: $\chi^2 = 5.00$, df = 2, $p = 0.082$). There was also no difference between sexes ($\chi^2 = 0.271$, df = 1, $p = 0.602$). Mean *A. vasorum* intensity over both years was not related to host age, sex, or body fat index (model: $F_{[21, 72]} = 1.45, p = 0.140$) (Tables 6, 7), nor was it related to larval output (ln(number *A. vasorum* larvae/g dry feces) = $-0.053\sqrt{A.\ vasorum\ \text{intensity} + 0.5} + 3.755$, adjusted $r^2 = -0.006$, $F_{[1, 16]} = 0.91, p = 0.355$). Also, there were no relationships between the numbers of *A. vasorum* larvae and age class, sex, and body fat index (model: $F_{[13, 19]} = 0.89, p = 0.597$) (Tables 7, 8), or omental fat ratio (ln(number *A. vasorum* larvae/g dry feces) = -0.041(omental fat ratio) + 3.601, adjusted $r^2 = -0.029$, $F_{[1, 17]} = 0.50, p = 0.490$).

Interaction between *Crenosoma vulpis* and *Angiostrongylus vasorum*

As adult *C. vulpis* intensity differed between years, they were treated separately. Of the 163 foxes in the *A. vasorum* positive regions, 40% ($n = 65$) had dual infections (Table 14). There was no significant relationship between the intensities of *C. vulpis* and *A. vasorum* in either of the 2 years (year 1: ln(*C. vulpis* intensity) = $0.048\sqrt{A.\ vasorum\ \text{intensity} + 0.5} + 7.074$, adjusted $r^2 = -0.030$, $F_{[1, 33]} = 0.01, p = 0.913$; year 2: ln(*C. vulpis* intensity) = $0.538\sqrt{A.\ vasorum\ \text{intensity} + 0.5} + 6.225$, adjusted $r^2 = 0.044$, $F_{[1, 28]} = 2.34, p = 0.137$). Also, for each species, the mean intensity between single and dual infections was compared within the *A. vasorum* positive regions (Table 15, Figs. 7, 8). In year 1, the mean intensity of *C. vulpis* was higher in dual (412 ± 107.1) than in single infections (228 ± 63.3) ($U = 715.50, p = 0.041$), but did not differ in year 2 ($U = 140.00, p = 0.265$). Mean intensity of *A. vasorum* over both years did not differ between single (53 ± 9.6) and dual infections (80 ± 10.0) ($F_{[1, 90]} = 2.63, p = 0.108$).

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Table 14. Comparison of the number of red foxes (*Vulpes vulpes*) infected with *Crenosoma vulpis* and *Angiostrongylus vasorum* from *A. vasorum* positive regions (NEC, SCBP, and AP) of Newfoundland during the 2000-2002 trapping seasons.

	Number of foxes with *C. vulpis*	Number of foxes without *C. vulpis*	Total
Number of foxes with *A. vasorum*	65 (74.5)	67 (57.5)	132
Number of foxes without *A. vasorum*	27 (17.5)	4 (13.5)	31
Total	92	71	163

Note: North East Coast (NEC); South Coast/Burin Peninsula (SCBP); and Avalon Peninsula (AP). Observed number of foxes are shown with expected numbers in brackets. Trapping season is October-February.

Table 15. Mean intensity of *Crenosoma vulpis* and *Angiostrongylus vasorum* in red foxes (*Vulpes vulpes*) with single and dual infections in *A. vasorum* positive regions (NEC, SCBP, and AP) of Newfoundland during the 2000-2002 trapping seasons.

	Mean intensity of *C. vulpis*				Mean intensity of *A. vasorum*		
Nematodes present	Number of foxes[1]	Year 1	Number of foxes[1]	Year 2	Nematodes present	Number of foxes[1]	Total
C. vulpis only	55	228 ± 63.3 (1-3352)	12	216 ± 59.2 (14-724)	*A. vasorum* only	27	53 ± 9.6 (3-217)
C. vulpis (with *A. vasorum*)	35	412 ± 107.1 (1-3503)	30	204 ± 48.9 (1-1049)	*A. vasorum* (with *C. vulpis*)	65	80 ± 10.0 (1-379)

Note: North East Coast (NEC); South Coast/Burin Peninsula (SCBP); and Avalon Peninsula (AP). Intensity values shown are the mean intensity ± standard error; the ranges are in brackets. Trapping season is October-February. Year 1 = Oct. 2000-Feb. 2001. Year 2 = Oct. 2001-Dec. 2001.
[1] - Includes infected animals only.

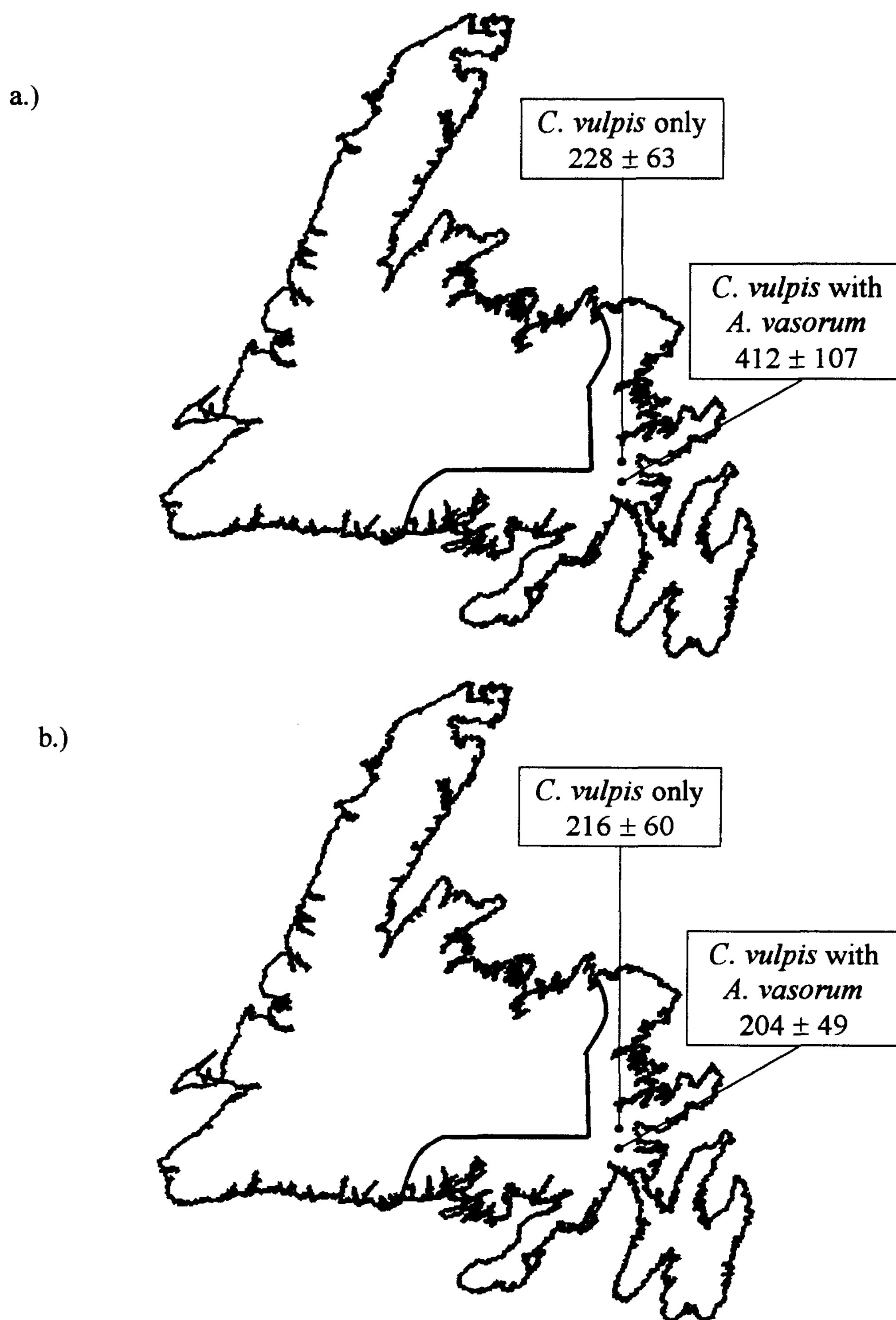

Fig. 7. Mean intensity (± S.E.) of *Crenosoma vulpis* from areas where it occurs with and without *Angiostrongylus vasorum* in different regions of Newfoundland. a.) year 1 (Oct. 2000-Feb. 2001), b.) year 2 (Oct. 2001-Dec. 2001).

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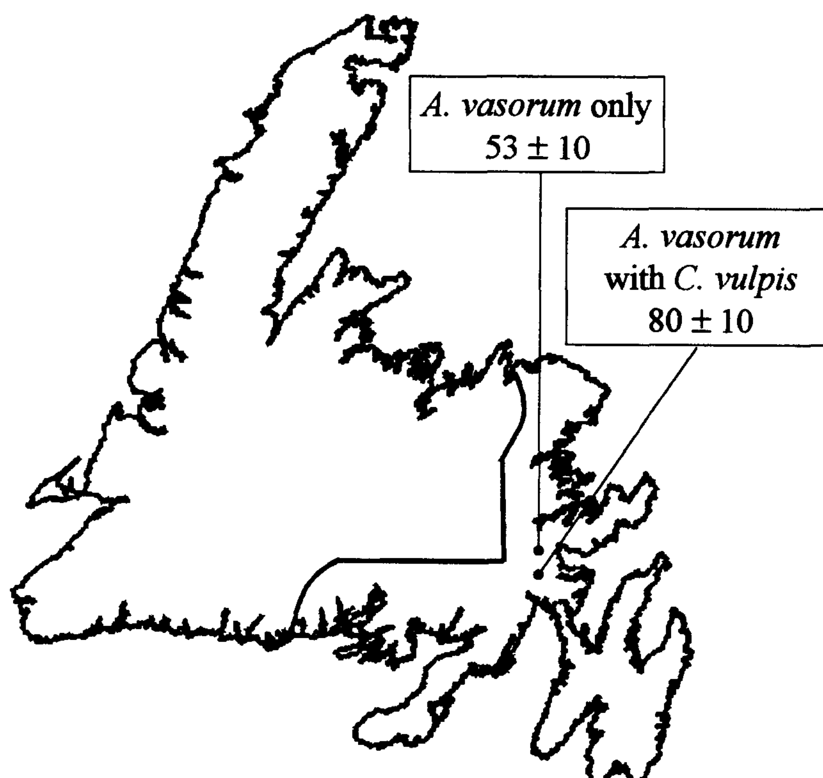

Fig. 8. Mean intensity (± S.E.) of *Angiostrongylus vasorum* with and without *Crenosoma vulpis* in Newfoundland during the 2000-2002 trapping seasons.

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Within the *A. vasorum* positive regions, 65 foxes had dual infections, 67 had *A. vasorum* only, 27 had *C. vulpis* only, and 4 had neither (Table 14). A G-test showed significant negative interaction between the two parasites ($G_{c[1]}$ = 14.59), as there were fewer animals with dual infections than expected (74.5). As *A. vasorum* distribution is sparse within the North East Coast and South Coast/Burin Peninsula regions, they were excluded from a second G-test. There was no interaction between *C. vulpis* and *A. vasorum* on the Avalon Peninsula which had 58 foxes with dual infections, 25 with *C. vulpis* only, 8 with *A. vasorum* only, and 3 that were uninfected ($G_{c[1]}$ = 0.10).

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Discussion

Crenosoma vulpis is distributed throughout Newfoundland where mean winter temperatures (December to February) range from 0 to −12°C (Water Resources Atlas of Newfoundland 1992, Banfield 1993). Based on its broad global distribution, Snyder (1985) suspected that *Crenosoma* spp. can probably survive a wide range of environmental conditions, including freezing. L_1 of *C. goblei*, the lungworm of racoons (*Procyon lotor*), can survive freezing for 5-14 months at −25°C (Snyder 1985). Although the ability of *C. vulpis* larvae to survive freezing has not been studied in detail, preliminary observations in this study found larvae alive after being frozen at −20°C for 3-7 months. These initial findings and the knowledge that related species withstand freezing, probably explain its island-wide distribution.

The distribution of *A. vasorum* in Newfoundland is not limited to the Avalon Peninsula as previously suspected (Whitney 1998), but extends north to the Bonavista Peninsula and southwest to the Burin Peninsula. Its absence from the rest of the island might be explained by its recent introduction, or by climate. The Avalon Peninsula is separated from the rest of the island by a narrow, 6-km wide isthmus. Although it may act as a barrier to larger animals such as caribou (*Rangifer tarandus tarandus*) by restricting their movement (Ball et al. 2001), it is unlikely to have had an effect on the dispersal of infected red foxes. European foxes (*V. vulpes*) were introduced to eastern North America by early settlers for sport hunting as early as 1750 (Churcher 1959). Kamler and Ballard (2002) believe that prior to European introduction, the predominant fox colours in North America were the cross and silver phases, and that the red phase did not become common until European animals were imported. Up to 90% of foxes in Newfoundland

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exhibit the red phase (Northcott 1974) indicating the presence of European stock that could have brought *A. vasorum*. This does not, however, explain the absence of *A. vasorum* from other North American locations to which European red foxes were also imported. The Newfoundland fur-ranching industry did not begin importing red foxes from Europe until 1981 (pers. com., Mr. Wiseman, President, Newfoundland and Labrador Fur Breeders Association, St. John's, NL), eight years after *A. vasorum* was first reported (Smith and Threlfall 1973). *Angiostrongylus vasorum* might also have been introduced to the island with domestic dogs imported from Europe. Although its mode of introduction to Newfoundland remains unknown, *A. vasorum* has most likely existed there long enough to disperse to the rest of the island unless restricted by another limiting factor such as temperature. Further study is needed, however, to determine if time is important in determining the distribution of *A. vasorum*.

Angiostrongylus vasorum does not occur in regions of Newfoundland where mean winter temperatures drop below approximately −4.0°C (Water Resources Atlas of Newfoundland 1992). Prior to 1992, the mean winter temperatures in the northern regions of the Avalon Peninsula were between −4.1 and −6.0°C (Water Resources Atlas of Newfoundland 1992), but since then have increased to −3.8°C (Canadian Climate Service, Environment Canada 2002). Globally, *A. vasorum* seems to be absent from areas with colder climates (Climatic Atlas of Europe 1970). Within France, for instance, *A. vasorum* infection is more common in the south where the climate is milder (Dorchies 1976), and Martin et al. (1993) noted that many reports are from "wet and mild" climates. In the laboratory, all L_1 frozen in feces at −20°C were dead when thawed 24 hours later. Bourdeau (1993) found that even at 18 to 25°C, most L_1 died quickly, with very few surviving longer than 3 weeks. The inability to survive freezing temperatures may restrict *A.*

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vasorum to the warmer areas of southeastern Newfoundland. The distribution of *A. vasorum* is unlikely to be limited by rainfall. Areas of mean annual precipitation ranging from 1100-1300 mm (Water Resources Atlas of Newfoundland 1992) include and extend northward and westward of *A. vasorum*'s distribution.

The prevalence of *C. vulpis* varies greatly throughout its range. The overall prevalence in Newfoundland was 87%, much higher than previously reported elsewhere. Within Europe, Spain (3%) (Alvarez et al. 1992), Italy (3%) (Poli et al. 1985) and Germany (6%) (Steinbach 1993) report the lowest prevalences, while Austria (25%) (Lassnig et al. 1998), Denmark (29%) (Willingham et al. 1996), the former Soviet Union (39%) (Chertkova 1962), and England (57%) (Watkins and Harvey 1942) have the highest. North American prevalences ranged from 21% in New York State (Goble and Cook 1942, Zeh et al. 1977), 54% in New Brunswick and Nova Scotia (Smith 1978) to 83% in Prince Edward Island (Conboy 1996), are still lower than those in Newfoundland. Two previous studies in Newfoundland (Threlfall 1969, Smith and Threlfall 1973) examined too few foxes ($n = 4$) to provide representative data. Few reports exist on *C. vulpis* in coyotes, however, using a lung flush technique similar to that used in this study, 38% of coyotes in Prince Edward Island were infected (Conboy 1996, pers. com., Conboy, UPEI), the same prevalence as in 8 coyotes in Newfoundland (38%). Prevalence in domestic dogs is apparently much lower than in wild foxes or coyotes. A study of 310 dogs in Prince Edward Island found only 3% to be infected (Bihr and Conboy 1999).

The overall mean intensity of *C. vulpis* in foxes in Newfoundland (230 ± 20.8; 1-3503) was higher than previously reported in other locations. Mean intensities in wild foxes varied between 6 (3-12) (mean followed by range in brackets) in Italy (Poli et al. 1985), and 24 (1-84) in

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England (Watkins and Harvey 1942). Goble and Cook (1942) retrieved 50 and 100 worms from two foxes in New York State but suspected that the actual intensity was up to 3 times higher. Coyotes in Newfoundland had a mean intensity of 16 ± 10.2 (4-36) *C. vulpis*, while in Prince Edward Island the intensity ranged from 1-4 (Conboy 1996). Mean intensity in dogs in Prince Edward Island was 11 ± 13 (1-35) (Bihr and Conboy 1999).

The greater numbers of *C. vulpis* recovered in this study may be, in part, a result of using the lung flush technique rather than manual dissection of the airways as has been employed by previous researchers. The technique of flushing water through the right ventricle, as originally developed by Oakely (1980), retrieved 99% of *Dictyocaulus viviparus* from the lungs of cattle (*Bos taurus*). Flushing through the left ventricle, as modified here, is probably similarly effective. Up to 3503 *C. vulpis* were recovered from one fox. Far fewer worms were recovered from dogs and coyotes which may be innately less susceptible. Also, a different lifestyle (i.e., urban vs rural) may give dogs fewer opportunities to contact infective intermediate hosts. Bihr and Conboy (1999) found that infected dogs living in rural areas had higher mean intensity (12 ± 14) and prevalence (5 %) values than those in urban centres (1 and 1%, respectively)

Of the gastropods present in Newfoundland, at least 2 species, *Arion circumscriptus* and *A. hortensis* are suitable intermediate hosts for *C. vulpis* (Anderson 2000). Transmission may not involve vertebrate paratenic hosts as larvae failed to encapsulate in rats and mice (Anderson 2000). However, *C. mephitidis* of skunks (*Mephitis mephitis*) can use amphibians, reptiles and meadow voles (*Microtus pennsylvanicus*) (Anderson 2000). If *C. vulpis* uses paratenic hosts as does *C. mephitidis*, Newfoundland has several potential candidate species, including meadow voles which are abundant (Northcott 1974), and 4 species of amphibians (Maunder 1983).

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The prevalence of *A. vasorum* in Newfoundland was 56% over its entire distribution, similar to previous reports in England (0.3-42 %) (Ash 1968, Simpson 1996), Spain (2%) (Alvarez et al. 1992), Italy (27%) (Poli et al. 1984, Poli et al 1985, Poli et al. 1991), and Denmark (2-80%) (Guildal and Clausen 1973, Bolt et al. 1992, Willingham et al. 1996). The mean intensity of *A. vasorum* in foxes in Newfoundland was 72 ± 7.6 (1-379) which was higher than that reported in Italy (18, range 3-50) (Poli et al. 1984, Poli et al. 1985). Experimentally infected dogs given 150 to 10,000 L_1 had between 1 and 2000 worms, but most had between 50 and 100 (Guilhon 1966, Mishra and Cens 1971, Prestwood et al. 1981, Lima et al. 1994). Intensities ranged from 5 to 184 in naturally infected dogs (Roche and Kelliher 1986, Martin 1989, Perry et al. 1991, Koch et al. 1992). It has been suggested that foxes infected with *A. vasorum*, which have fewer clinical signs and less significant pathology, are less severely affected than dogs (Simpson 1996).

Several terrestrial gastropods are known to be suitable intermediate hosts of *A. vasorum*, of which at least two slug species, *Arion ater* and *Deroceras laeve*, occur in Newfoundland (Maunder 1985). *Arion ater* has been observed feeding on dog feces (Simpson and Neal 1982, Simpson 1996), and within Newfoundland, *D. laeve* is especially abundant in regions where *A. vasorum* occurs (Lankester and Fong 1996). Although it has not yet been determined for *A. vasorum*, infective L_3 of many other metastrongyloids of carnivores encyst in the livers of rodent and insectivore paratenic hosts (Lankester and Anderson 1966). These small mammals probably consume more gastropods than do red foxes. Through biomagnification, a fox could acquire many infective larvae by eating a small number of paratenic hosts. Small mammals constitute a large part of red fox diet, although shrews may be preyed upon less than rodents (Fairley 1970,

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Brosset 1974, Northcott 1974, Richards 1977, Reynolds 1979, Hewson and Leitch 1983). The common shrew (*Sorex cinereus*), and 8 rodent species occur in Newfoundland, including the meadow vole (Northcott 1974).

In addition to mammals, preliminary work has indicated that the common frog, *Rana temporaria*, may act as a paratenic host for *A. vasorum* (Bolt et al. 1993, Tharaldsen and Vollset 1996). L_3 of *Angiostrongylus cantonensis,* the closely related neurotropic heartworm of rats, has been found in the tissues of 53% of *Hyla aurea* (Ash 1968). Within Newfoundland, there are a number of amphibians but only the green frog, *Rana clamitans,* lives within *A. vasorum* positive regions (Maunder 1983). It has been suggested that L_1 may develop to the infective-stage in frogs in the absence of the usual gastropod intermediate hosts (Bolt et al. 1993), but confirmation of this report is necessary.

Fox lungs heavily infected with only *C. vulpis* showed little grossly visible pathology despite the rather severe histopathology, including interstitial pneumonia, and bronchitis, reported by authors elsewhere (Stockdale and Hulland 1970, Poli et al. 1985, Shaw et al. 1996). Foxes infected with *A. vasorum* showed conspicuous areas of discolouration and consolidation concentrated at the margins of the infected lobes, a pattern noted in dogs and foxes by several researchers (Roche and Kelliher 1986, Poli et al. 1991). Greater blood flow to the margins of the lobes (West et al. 1964, Bwangamoi 1974) may concentrate the eggs and L_1 at the edges, creating this pattern of gross pathology. *Angiostrongylus vasorum* is also thought to infect the diaphragmatic lobes more frequently than the others (Bwangamoi 1974, Perry et al. 1991, Poli et al. 1991, Simpson 1996). Foxes examined from Newfoundland had equal rates of infection in all lobes. However, the combined posterior lobe groups (47 ± 5.4; 1-302) had more worms than the

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anterior (25 ± 2.5; 1-96), possibly due to differential blood flow to the lobes. There was no difference between right (39 ± 4.2: 1-189) and left (32 ± 3.8; 1-186) lobe groups.

Although French heartworm has been frequently described from the right ventricle of the heart (Rosen et al. 1970, Bwangamoi 1972, Lynch 1977, Poli et al. 1985, Roche and Kelliher 1986, Patteson et al. 1987, King et al. 1994), there were significantly more *A. vasorum* in the pulmonary arteries of the lungs (75 ± 8.7; 1-375) than in the right ventricle (10 ± 1.9; 1-105). Although 78% of infected foxes had at least 1 worm in the right ventricle, approximately 88% of total worms were actually found in the arteries.

Sufficient fibrosis, constriction and occlusion of pulmonary arteries by *A. vasorum* could cause an enlarged heart (Dodd 1973, Martin 1989, Lynch 1977, Poli et al. 1984, Perry et al. 1991, Poli et al. 1991, Koch et al. 1992, Patteson et al. 1993). An increase in heart mass would result in an increase in heart weight ratio. The mean heart weight ratio in *A. vasorum* infected foxes was 0.87 ± 0.020%, lower than in uninfected foxes (0.93 ± 0.013%). There was, however, no relationship between the number of *A. vasorum* and heart weight ratio, indicating that in foxes, the heart does not enlarge with increasing worm burden. Ventricular ratio was not affected by the number of *A. vasorum* even though infection in dogs and foxes can enlarge and thicken the right ventricle (Poli et al. 1984, Patteson et al. 1987, Perry et al. 1991, Koch et al. 1992). Furthermore, the ventricular ratio did not differ between uninfected foxes (4.02 ± 0.188) and those with *A. vasorum* (4.06 ± 0.284).

The numbers of *C. vulpis* adults decreased with fox age. In Newfoundland, the mean intensity of *C. vulpis* was 307 ± 29.8 in YOY, dropping to 79 ± 24.7 in YRLG and 69 ± 27.7 in adults. A similar decrease in the number of *C. vulpis* adults with age has also been observed in

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dogs (Bihr and Conboy 1999). Dogs less than 12 months had 18.2 ± 18.2 worms while animals 1 year and older had 6.7 ± 7.2 (Bihr and Conboy, 1999). In foxes, the average number of worms decreased from 42 in 7- to 9-month-olds to 1.7 in those older than 2 years (Watkins and Harvey 1942). A mean intensity of 84 in foxes younger than 1 year decreased to 16 in animals 1 year and older (Conboy 1996). Puppies and fox kits may be more likely to consume snails and slugs than adults (Richards 1977), suggesting that kits could have an increased exposure to infective larvae. As well, young foxes may acquire a partial immunity following their first exposure since experimentally infected foxes have less severe infections when reinfected with *C. vulpis* (Anderson 1971). Also, *C. vulpis* are relatively short-lived, surviving approximately 33 weeks in foxes (Anderson 1971). If older foxes consume few infective larvae and do not replace adult *C. vulpis*, the mean intensity would decrease with age. Lower numbers in older foxes could therefore be due to both acquired immunity to reinfection and changing food habits, although reducing the amount of slugs in the diet would be of less importance if paratenic hosts are involved.

The intensity of *A. vasorum* rose quickly in YOY and remained unchanged with increasing age. Since *A. vasorum* is known to be long-lived (Mishra and Cens 1971), those present are probably obtained early in life and an immune response may prevent reinfection. As the number of worms did not accumulate with age, the immune response may be sufficient to restrict *A. vasorum* to a 'threshold' or maximum intensity. *Angiostrongylus vasorum* produced larvae for 9 years in an experimentally infected dog (Mishra and Cens 1971). The oldest infected foxes in this study were 8.5 years old; thus, if the infections were acquired as kits, foxes could carry the same worms for their entire lifetime.

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In Newfoundland, the prevalence of neither *C. vulpis* nor *A. vasorum* were related to host sex which contrasts with other studies. A study of wild foxes in Denmark found 33% of males and 6% of females infected with *C. vulpis*, while 48% of males and 22% of females were infected with *A. vasorum* (Willingham et al. 1996). Furthermore, *A. vasorum* were found in 28% of male and 16% of female foxes in New York State (Goble and Cook 1942).

Crenosoma vulpis and *A. vasorum* intensities were not related to either body fat index or omental fat ratio. This is in contrast to studies which demonstrate that health or body condition often decreases with parasitic infection. For instance, the severity of mange caused by *Sarcoptes scabiei* negatively affected body condition in foxes (Newman et al. 2002); in severe infections, the body mass and back fat depth were lower compared to those with light infections. Also, the body mass of coyotes decreased as the number of *D. immitis* increased (Sacks and Blejwas 2000). In Newfoundland, the amounts of subcutaneous and omental fat in foxes were not affected by the intensity of *C. vulpis* or *A. vasorum* despite rather high intensities, especially of *C. vulpis*. As kidney fat and back fat thickness are considered the most accurate indicators of body fat in foxes (Winstanley et al. 1998), the body fat index and omental fat ratio used in this study may not have been sensitive enough to detect any changes in fox health. The lower intensity of *C. vulpis* in older animals might have been interpreted as a function of increased body fat, which increases with red fox age (Winstanley 2000). However, neither body fat index nor omental fat ratio were related to *C. vulpis* intensity.

The mean larval output of *C. vulpis* in foxes was 276 ± 65.5 larvae/g dry feces, with one animal producing up to 6279 larvae/g dry feces. Few reports exist on larval *C. vulpis* output, however an output of 211 larvae/g feces was observed from a domestic dog (Cobb and Fisher

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1992). The larval output in foxes did increase with intensity of adult worms, but the regression explained very little of the variability in the data. Although this model is weak, others have found similar relationships. Watkins and Harvey (1942) determined that despite large variability in larval output between fecal samples, *C. vulpis* larval output did increase with worm burden. One animal with 11 adult worms produced 133 to 233 larvae/g feces while another with 84 adults produced 166 to 1166 larvae/g feces.

In Newfoundland, the mean larval output of *A. vasorum* in foxes was 36 ± 7.9 larvae/g dry feces with a maximum of 136, which is considerably lower than reported in dogs. Data on larval *A. vasorum* output from dogs is based either on case studies of individual naturally infected dogs, where output ranged from 150 to 280,000 larvae/g feces (Jacobs and Prole 1975, Dodd et al. 1976, Martin 1989, Bolt et al. 1992, Martin et al. 1993), or on experimentally infected dogs which passed 7000 to 15,000 larvae/g feces (Guilhon 1966, Rosen et al. 1970). In these studies, however, there appears to be no relationship between numbers of adult *A. vasorum* and larval output. Slomke et al. (1995) suggested that any correlation between the number of female meningeal worms (*Paraelaphostrongylus tenuis*) and the number of larvae passed in the feces of white-tailed deer (*Odocoileus virginianus*) could be obscured by any of several factors including season, age of infection, and degree of immune response.

The larval output of *C. vulpis* in foxes was higher in YOY than in animals older than 1.5 years. It has been observed that larval output of some nematode species decreases as the host ages (Festa-Bianchet 1991, Ball et al. 2001) possibly due to reduced reproduction by older worms, or an increased immune response to the eggs and larvae developing in the lungs (Slomke et al. 1995). The larval output of *A. vasorum* did not decrease with age and the larval outputs of

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both *C. vulpis* and *A. vasorum* were not related to host sex, omental fat ratio or body fat index.

There was no linear relationship between numbers of *C. vulpis* and *A. vasorum*. Within the *A. vasorum* positive regions of Newfoundland, the prevalence of dual infection in foxes was 40%. In Denmark, 13% of foxes were infected with both *C. vulpis* and *A. vasorum* (Willingham et al. 1996). Although *C. vulpis* and *A. vasorum* both require intermediate gastropod hosts, the lack of an apparent relationship between the intensities of the two nematodes suggests that each may be transmitted by different host species in the wild. Moreover, the mean intensity of both *C. vulpis* and *A. vasorum* did not differ between single and dual infections. Infection with certain intestinal nematodes, such as *Haemonchus contortus*, *Trichostrongylus contortus*, or *T. colubriformis* in sheep (*Ovis aries*), can prevent further infection by the same or closely related parasites (Stewart 1955, Barger 1984). If *A. vasorum* protected against subsequent *C. vulpis* infection, animals with single *C. vulpis* infections would be expected to have greater worm burdens than those with dual infections, which did not occur. Furthermore, there was no measurable interspecific competition between *A. vasorum* and *C. vulpis*. Initially, there appeared to be a negative interaction between the parasites within the *A. vasorum* positive regions. However, *A. vasorum* was absent from the majority of the North East Coast and the South Coast/Burin Peninsula regions, meaning that foxes there would be more likely to be infected by *C. vulpis* than by *A. vasorum* which could create spurious results. Therefore, the Avalon Peninsula was considered independently as both *C. vulpis* and *A. vasorum* were equally wide-spread there. There was no apparent interaction between the parasites on the Avalon Peninsula, indicating the prior result had been an artifact of low *A. vasorum* prevalence for much of its distribution. It is unlikely that either *C. vulpis* or *A. vasorum* offered reciprocal or cross-protective immunity

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against infection with the other as the prevalences and mean intensities in dual infections were no different than in single infections.

A closely related heartworm, *Angiocaulus gubernaculatus*, was recently reported from the island fox on the California Channel Islands (Faulkner et al. 2001). This species was originally described from badger and placed in the genus *Angiostrongylus* (Dougherty 1946). It was subsequently transferred to the new genus *Angiocaulus* by Schulz in 1951 (Skrjabin et al. 1952). However, some researchers have removed *A. gubernaculatus* from *Angiocaulus* and returned it to *Angiostrongylus* (Drozdz 1970, Kontrimavichus and Delyamure 1979). Also, *Angiostrongylus raillieti*, first described from the crab-eating fox (*Cerdocyon thous*) in Brazil (Travassos 1927), has been considered by some to be a member of the genus *Angiocaulus* (Ubelaker 1986), while others suspect it might be a synonym of *A. vasorum* (Rosen et al. 1970). Clearly, careful examination of all three species is needed to clarify their relationships and validity. Further research might demonstrate that *A. gubernaculatus* and *A. vasorum* are in fact the same species.

In summary, it was determined that *C. vulpis* is distributed over the entire island of Newfoundland while *A. vasorum* is restricted to the southeast, possibly because its free-living L_1 cannot survive freezing below −4°C. Despite their high mean intensities, neither nematode had a detectable effect on the health of foxes based on the indices measured in this study. Finally, there appears to be no interaction between *C. vulpis* and *A. vasorum* when in the same individual host.

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