Echinococcus granulosus (CESTODA: TAENIIDAE) INFECTIONS IN MOOSE (*Alces alces*) FROM SOUTHWESTERN QUEBEC

BY

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Echinococcus granulosus infections in moose (*Alces alces*)

ABSTRACT

Investigation of the distribution of Echinococcus granulosus (Cestoda: Taeniidae) in moose (Alces alces) of southwestern Quebec revealed a distinct pattern of infection in this intermediate host species. Prevalence averaged 44 percent, with fluctuations between certain years. Positive correlations between moose age and the intensity, mean cyst weight and biomass of infection suggest a pattern of continual parasite acquisition and growth. The distribution of cyst sizes within individual moose provides circumstantial evidence of cyst-cyst interaction. Necropsy of wolves (Canis lupus) from the same study area confirms this species' role as the definitive host of E. granulosus in this sylvatic cycle.

ABREGE

Une étude de la distribution d'Echinococcus granulosus (Cestoda: Taeniidae) chez une population d'orignaux (Alces alces) vivant au sud-ouest du Québec a démontrée un mode précis d'infection chez cet hôte intermédiaire. La moyenne de la prévalence est de 44 pourcent mais elle est sujette à des fluctuations annuelles. Des corrélations positives entre l'âge de l'orignal et l'intensité, la moyenne des poids des kystes, et la biomasse de l'infection suggère une acquisition continuelle du parasite ainsi qu'une croissance de ce même parasite. La distribution des kystes de différents volumes chez un même hôte nous fournit l'évidence d'une interaction existante entre les kystes. La nécropsie de loups (Canis lupus) de la même aire d'étude confirme que le loup est bien l'hôte définitif d'E. granulosus dans ce cycle sylvatique.

Suggested short title:

Echinococcus granulosus infections in moose (*Alces alces*)

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GLOSSARY

ECOLOGICAL TERMS

PREVALENCE: Number of individuals of a host species infected with a particular parasite species ÷ Number of hosts examined.

INTENSITY: Number of individuals of a particular parasite species in each infected host in a sample.

MEAN INTENSITY: Total number of individuals of a particular parasite species in a sample of a host species ÷ Number of infected individuals of the host species in the sample (= Mean number of individuals of a particular parasite species per infected host in a sample).

ABUNDANCE: Total number of individuals of a particular parasite species in a sample of hosts ÷ Total number of individuals of the host species (infected + uninfected) in the sample (= Mean number of individuals of a particular parasite species per host examined).

(From Margolis et al., 1982)

PARASITOLOGICAL TERMS

SITE: The tissue, organ or part of the host in which a parasite is found.

CYST WEIGHT: The weight in grams of an individual cyst.

BIOMASS: The weight in grams of all cysts in the lungs of a particular moose.

TO M.J.W.

CHAPTER I. INTRODUCTION

"Parasites of wild animals have traditionally been regarded as ubiquitous and interesting commensals which provide challenging and fascinating thesis problems for aspiring parasitologists" (Davis and Anderson, 1971). This general attitude, which characterized much work on wildlife disease and management throughout the first half of this century, has been radically altered over the past few decades. The view, once commonly accepted, that wildlife parasites were very well adapted to their hosts and thus caused little pathology, has been falcified as more and more studies reveal that parasites are indeed significant pathogens of wild animals. Classic examples include the revelation of the parasitic cause of neurologic disease in moose (Alces alces L.) (Anderson, 1971), elaeophorosis in elk (Cervus canadensis Erxleben) (Adcock et al., 1965), the lungworm-pneumonia complex in bighorn sheep (Ovis canadensis L.) (Buechner, 1960) and hookworm disease in fur seals (Callorhinus ursinus L.) (Olsen and Lyons, 1965).

Much has since become known about the taxonomy, morphology and life cycles of wildlife parasites. In addition, some of the pathologic effects of such parasites on the individual host have been examined (Honess, 1942; Lack, 1954; Adcock and Hibler, 1969; Pybus and Samuel, 1980). However, these studies provide little information about the effects of parasitic infections on the host population and hence, the significance of parasitic disease in natural populations is poorly understood.

This dearth of knowledge is largely due to the logistic and financial problems encountered in studying wild animals under field conditions. These ecological systems are largely intractable and thus, quantitative data on the impact of parasitic disease on wildlife are virtually unattainable. However, this does not mean that we cannot study the effects of parasitism in wild animals. Background information, on the biology and ecology of the host species, together with data on the distribution of a parasite within the host population and, where possible, laboratory studies of the effects of such infections on the individual host, can be used to gain considerable insight into the ecological significance of a given parasitic infection.

The cyclophyllidean cestode Echinococcus granulosus (Batsch, 1786) has a cosmopolitan distribution among a variety of intermediate and definitive hosts. In North America, however, the life cycle most commonly encountered involves a cervid intermediate host and a wild canid definitive host. As suggested by Sweatman and Williams (1963a), sylvatic echinococcosis was probably introduced to North America by the moose, which immigrated fairly recently to the new world. Other cervids such as elk and caribou (Rangifer tarandus L.) may also harbour this parasite (Rausch, 1967). However, it is evident that E. granulosus is firmly established in the boreal forest regions of this continent by mediation of the moose (Figure 1-1), which is the cervid most commonly found infected wherever it coexists with large canids (Sweatman and Williams, 1963a; Anderson and Lankester, 1974). Timber wolves (Canis lupus L.) (Figure 1-2) are the most common definitive host (Freeman et al., 1961; Holmes and Podesta, 1968) and are probably the

Figure 1-1. Moose (<u>Alces alces</u>) intermediate host of <u>Echinococcus granulosus</u>.

A. Adult male. (Photograph: F. Messier)

B. Adult female. (Photograph: F. Caron)

A

B

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Images en couleur

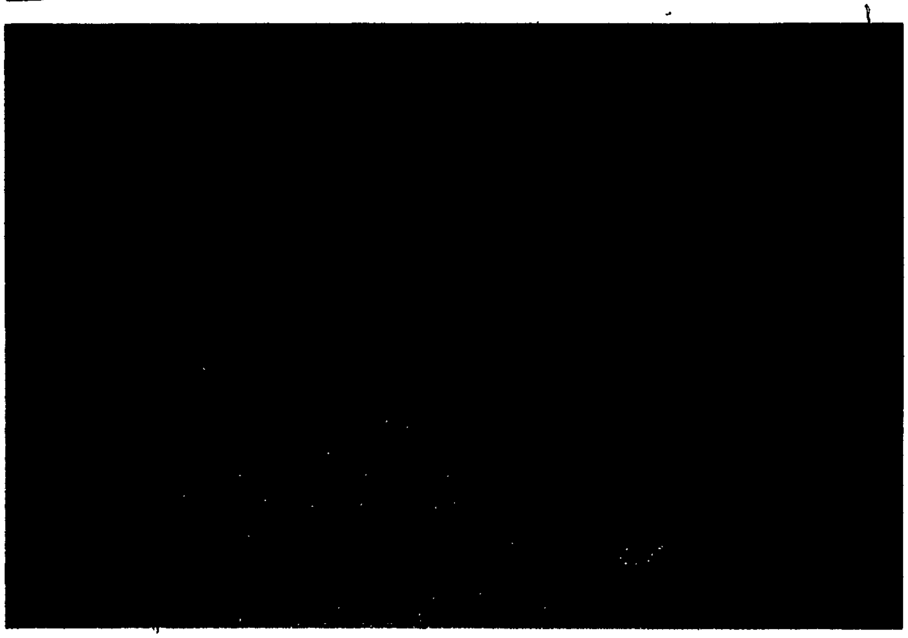
Figure 1-2. Wolf (Canis lupus) definitive host of Echinococcus granulosus.

A. Adult. (Photograph: F. Messier)

B. Wolf pack; a family and hunting unit. (Photograph: Fiennes, 1976)

A

B



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only important canid host of E. granulosus in the North American sylvatic cycle (Sweatman and Williams, 1963a).

Adult E. granulosus are three to six millimeters long and consist of a scolex and neck followed by three to four proglottids in successive stages of maturity. The scolex has a protrusible rostellum armed with one row each of large (40 to 49 μm) and small (30 to 42 μm) hooks (Olsen, 1974). From the adult in the wolf's intestine, eggs (30 by 38 μm) (Chandler and Read, 1964) are passed onto the ground and vegetation in the faeces. These eggs, under natural conditions in a temperate climate, may remain viable at least as long as one year (Batham, 1957; Sweatman and Williams, 1963b).

Moose may become infected by ingesting eggs in the faeces of infected wolves or on contaminated vegetation (Leiby and Dyer, 1971; Anderson and Lankester, 1974). The oncospheres, which measure about 28 μm (Heath, 1971), are liberated from their striated embryophores by the action of digestive juices and enzymes in the stomach and small intestine (Meyer and Olsen, 1975). Following penetration of the intestinal epithelium, the oncospheres enter either the venules (Meyer and Olsen, 1975) or the lymphatic lacteals (Heath, 1971). Upon reaching a suitable site, the oncospheres vesiculate into unilocular cysts. In moose, these cysts are found commonly in the lungs and rarely in the liver, spleen, heart or kidneys (Addison et al., 1979). Fibrosis occurs in the tissue surrounding a hydatid and neighbouring cells may undergo pressure atrophy as the cyst increases in size (Meyer and Olsen, 1975).

The cyst wall is composed of an outer laminative and inner germinative membrane (Noble and Noble, 1976). The mother hydatid gives rise to numerous brood capsules (Figure 1-3) and protoscoleces (Figure 1-4) by endogenous proliferation of the germinal epithelium (Leiby and Dyer, 1971). These may become free in the hydatid fluid and settle, whereupon they comprise a sediment which is referred to as hydatid sand. Brood capsules may produce daughter capsules with their own protoscoleces (Olsen, 1974). Thus, a single cyst may contain many thousands of larval tapeworms (Figure 1-5), each of which can develop into an adult (Figure 1-6) when ingested by the appropriate definitive host (Meyer and Olsen, 1975).

The present study describes the distribution of the hydatid cysts of E. granulosus in a population of moose from southwestern Quebec. Prevalence of infection in the coexisting wolf population is also examined. The ecological significance of this infection in the intermediate host is discussed.

Figure 1-3. Brood capsule with protoscoleces. (x64)

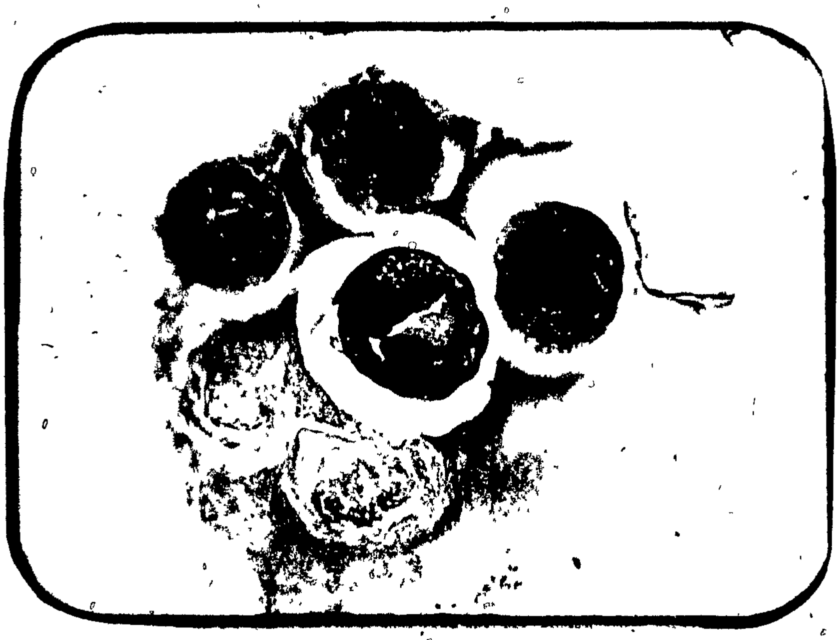
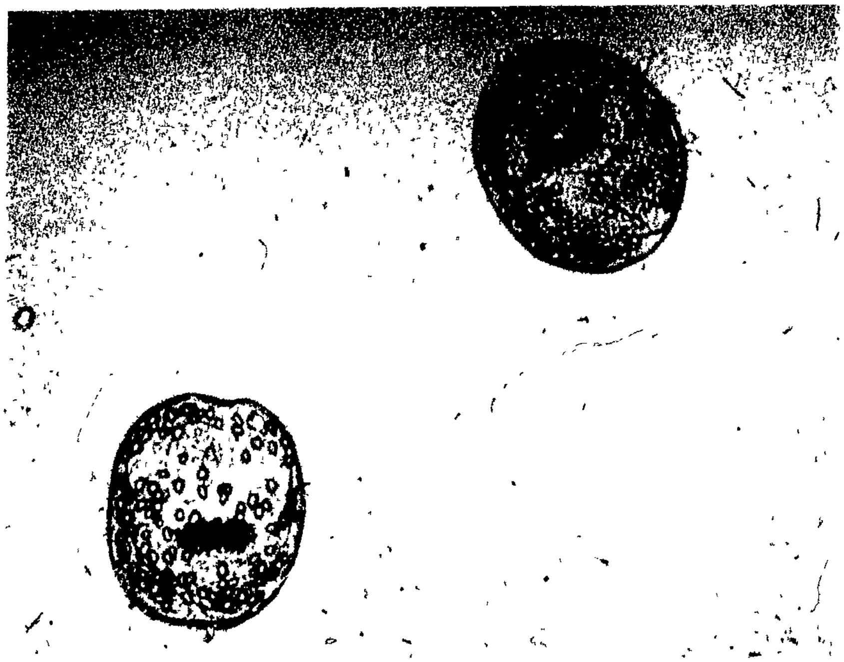


Figure 1-4. Protoscoleces from a hydatid cyst of <u>Echinococcus granulosus</u>.

A. Lateral view. (x100)

B. Enface view of rostellar hooks. (x126)

A



B

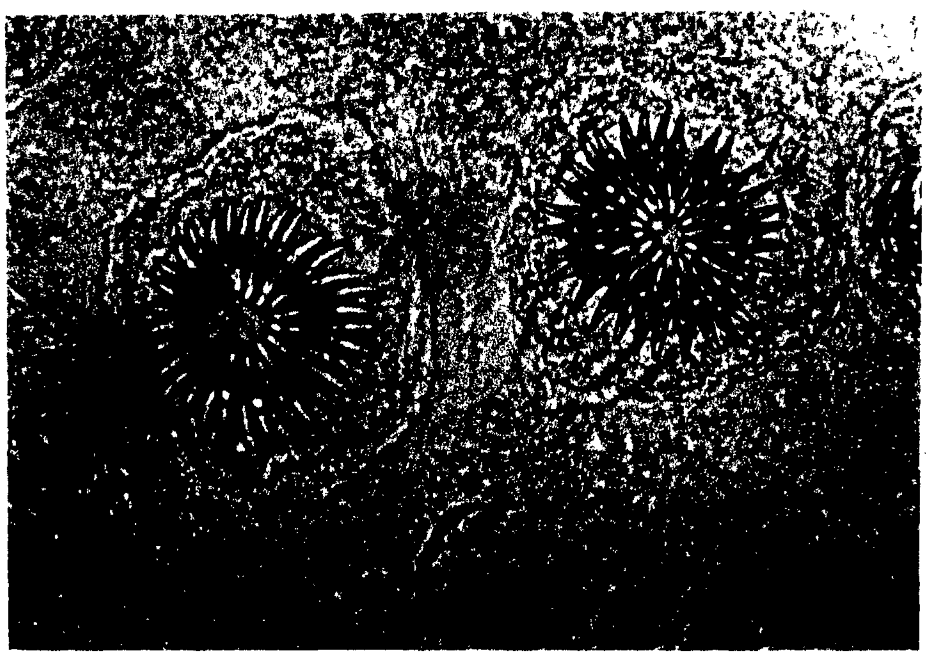
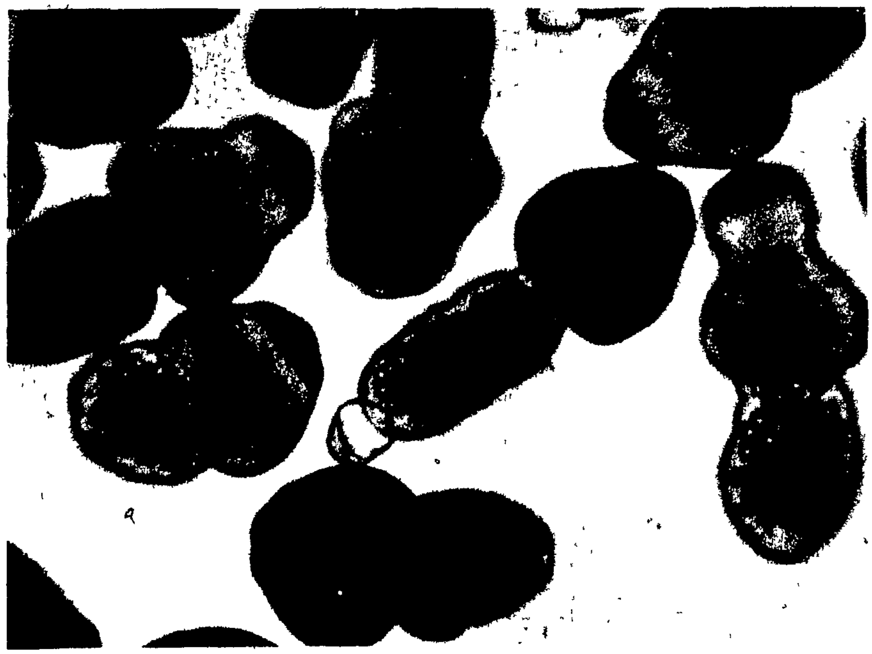


Figure 1-5. Evaginated protoscoleces of <u>Echinococcus granulosus</u>. (x40)

Figure 1-6. Young adult of <u>Echinococcus granulosus</u>. (x10)



CHAPTER II. THE STUDY AREAS

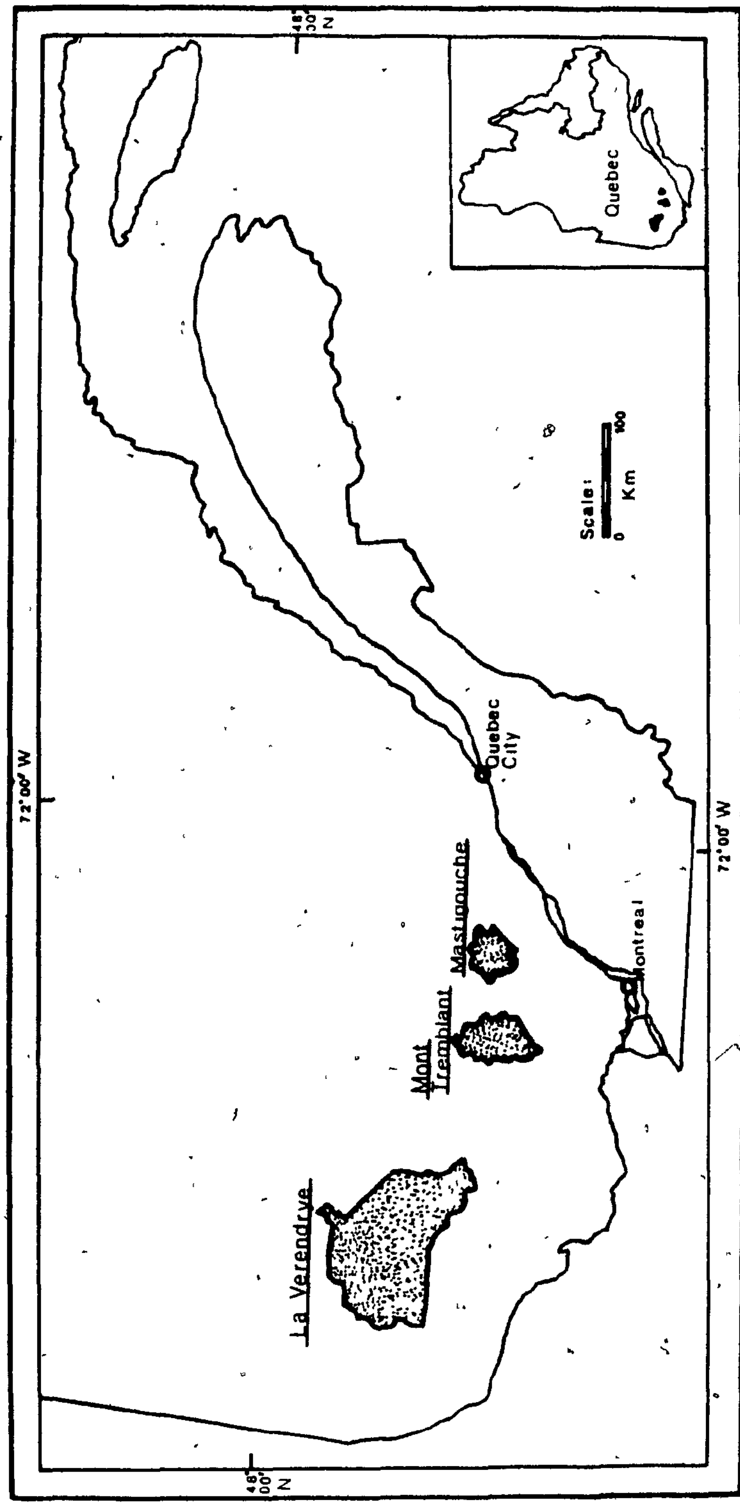
A. LOCATION

The three study areas, the Rouge-Matawin Reserve, the La Verendrye Reserve and the Mastigouche Reserve, are located in southwestern Quebec (Figure 2-1) and cover 1,635, 13,615 and 1,755 square kilometers respectively. The Rouge-Matawin Reserve was created, in 1981, from the northern half of Mont-Tremblant Park (2,564 square kilometers). The hunting zones of Mont-Tremblant Park were subdivided when the Rouge-Matawin Reserve was defined (Appendices 3-1 and 3-2). However, the actual area exploited during the annual moose hunt remained the same as in previous years. This region is hereafter referred to as the Rouge-Matawin Reserve.

B. CLIMATE

The climate of the three study areas is continental temperate, with certain characteristics of mountain climates in the higher elevations (Wilson, 1971; MLCP publication). Snowfall rarely exceeds 400 centimeters which corresponds to 87.5 to 100 centimeters on the forest floor (Brassard et al., 1974). The only study area in which snowfall was precisely measured was La Verendrye; the average accumulation was 85 to 90 centimeters (F. Messier, pers. comm.).

Figure 2-1. Map of southern Quebec indicating the location of the three study areas.


Quebec
Scale:
0
100
Km
Quebec City
Montreal
Mastigouche
Mont Tremblant
La Verendrye
72°00' W
48°00' N

C. HABITAT

The three study areas are located primarily within a boreal coniferous forest region (Rowe, 1959). These forests are dominated by balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss) and paper birch (*Betula papyrifera* Marsh.). The most southerly reaches of these reserves are characterized by a transition zone between the boreal forests and the decidious forests of the St. Lawrence lowlands. The main tree species occurring in this second forest zone include yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), balsam fir, red spruce (*Picea rubens* Sarg.), white spruce and red pine (*Pinus strobus* L.). The physiography is characterized by undulating hills (457 to 610 meters high), numerous small lakes and extensive water courses (MLCP publication) (Figure 2-2).

Logging operations are permitted in certain parts of the reserves. These logging activities produce localized areas of successional growth which improves the quantity and quality of available browse (deVos, 1962; Krefting, 1974). These habitat features provide the best potential for moose and mean moose densities range from 1.8 moose per ten square kilometers in the transitional zone, to 2.6 moose per ten square kilometers in the boreal forest region (Brassard *et al.*, 1974) (Figure 2-3).

Figure 2-2. Habitat of the study areas.

A. Aerial view of the La Verendrye Reserve.

B. Ground view of the Rouge-Matawin Reserve.

A

B

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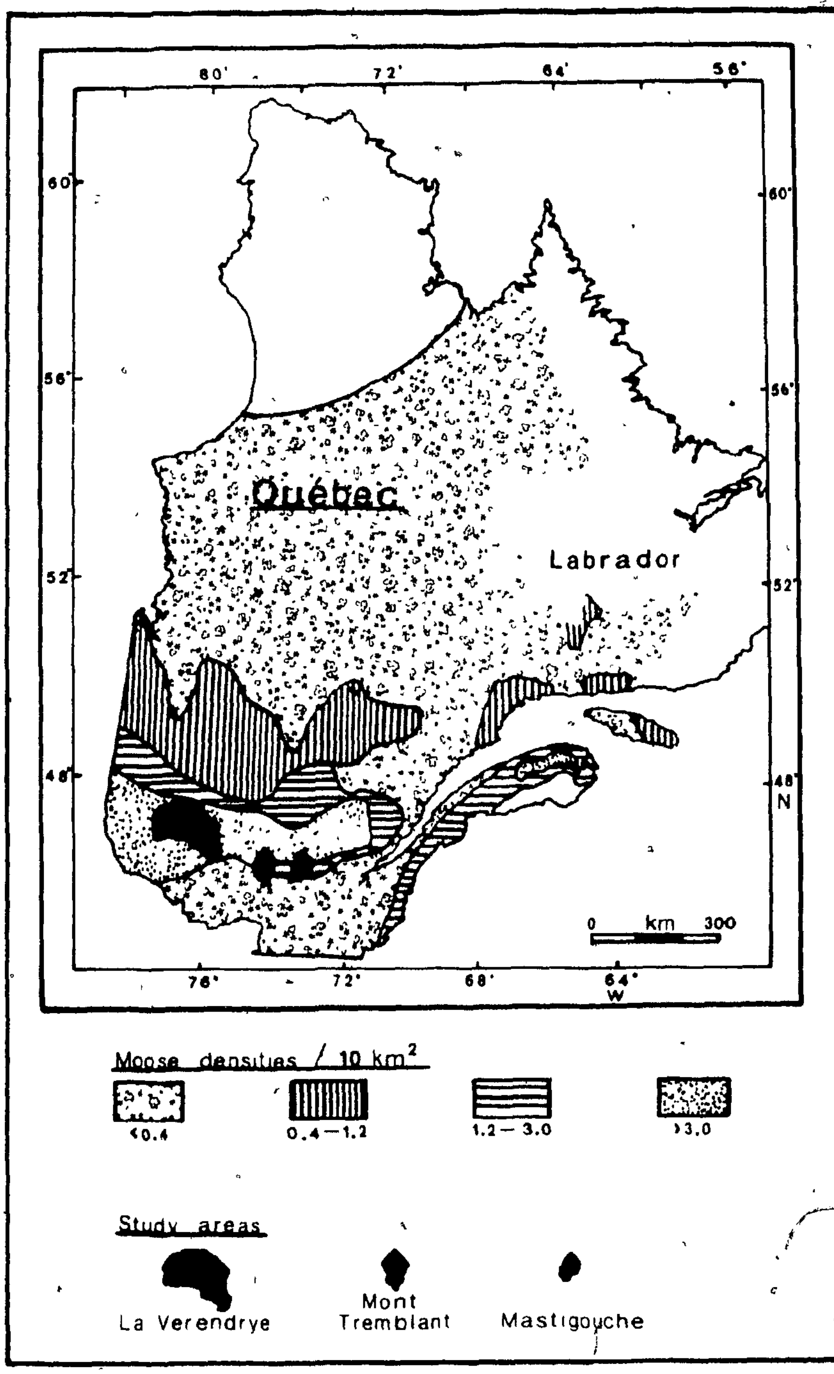
Figure 2-3. Map of Quebec showing location of the study areas in relation to regions of estimated moose densities. (from Brassard et al., 1974)


80°
72°
64°
56°
60°
56°
52°
48°
N
76°
72°
68°
64°
W
Québec
Labrador
0 km 300
Moose densities / 10 km²
<0.4
0.4—1.2
1.2—3.0
>3.0
Study areas
La Verendrye
Mont Tremblant
Mastigouche

D. FAUNA

In addition to moose and wolves, the fauna of the study areas includes: black bear (_Ursus americanus_ Pallus); red fox (_Vulpes vulpes_ L.); lynx (_Lynx canadensis_ Kerr); beaver (_Castor canadensis_ Kuhl); weasels and mink (_Mustela_ L. spp.); fisher and marten (_Martes_ Pinel spp.); otter (_Lutra canadensis_ Schreber); porcupine (_Erethizon dorsatum_ L.); hare (_Lepus americanus_ Erxleben); and various species of the cricetidae and zapodidae (native mice and rats). White-tailed deer (_Odocoileus virginianus_ Zimmerman) are present but not abundant as the location of the study area is coincident with the northern limits of this deer's range (Halls, 1978). Seasonal avian fauna include: partridge (_Perdix perdix_ L.); grouse (_Bonasa umbella_ L.); loons (_Gavia immer_ Brunnich) as well as various anatids, raptors and over 100 species of small birds. Some 200 species of fish are present in the lakes, rivers and streams.

CHAPTER III. Echinococcus granulosus INFECTIONS IN THE MOOSE

A. INTRODUCTION

The moose is the largest member of the deer family (Cervidae) and is one of North America's most highly prized game species. Mature bulls produce the largest antlers of any cervid and adults of both sexes yield up to 300 kilograms of meat. As such, the moose represents an extremely valuable wildlife resource. In Quebec alone, the moose hunt generates an estimated 50 million dollars annually in direct and indirect revenue (Ministère du Loisir, de la Chasse et de la Pêche (MLCP) personnel, pers. comm.). As a result, the biology and ecology of this species have been extensively studied (Murie, 1934; Peterson, 1955; Bédard et al., 1974). Parasitic diseases of moose were reviewed by Anderson and Lankester in 1974. Echinococcus granulosus has been reported from moose in Minnesota (Riley, 1939; Olsen and Fenstermacher, 1942; Karns, 1973); Isle Royale (Sweatman, 1952; Mech, 1970; Allen, 1979); Alaska (Rausch, 1952, 1959, 1967); Canada generally (Sweatman, 1952; Rausch, 1967); British Columbia (Ritcey and Edwards, 1958); Alberta (Stelfox, 1962; Samuel et al., 1976); Saskatchewan (Harper et al., 1955); Manitoba (Hadwen, 1932); Ontario (deVos and Allin, 1949; Addison et al., 1979) and Quebec (Rau and Caron, 1979). In a natural population, prevalence may range from zero to 68 percent (Samuel et al., 1976; Addison et al., 1979; Rau and Caron, 1979) (Table 3-1).

Table 3-1. Summary of North American reports of moose infected with *Echinococcus granulosus*.

LOCATION	PREVALENCE (%)	Number examined	REFERENCE
Alaska	24	(23/101)	Rausch, 1959
British Columbia	68	(23/34)	Ritcey and Edwards, 1958
Alberta	0	(0/22)	Samuel et al., 1976
Alberta	15	(6/39)	Samuel et al., 1976
Alberta	52	(32/62)	Samuel et al., 1976
Minnesota	42	(8/19)	Fenstermacher, 1937
Ontario	67	(36/54)	Addison et al., 1979
Quebec	58	(26/45)	Rau and Caron, 1979
Quebec	44	(214/489)	present study
Newfoundland	~~0~~	~~(0/10)~~	~~Threlfall, 1967~~

Resistance of the moose host to infection by E. granulosus has not been studied. Sweatman et al. (1963) investigated acquired immunity to E. granulosus in sheep (Ovis aries L.) and reported that a partial resistance does appear to occur after a high initial dose. In cotton rats (Sigmodon hispidus L.), preexisting subcutaneous cysts of Echinococcus multilocularis will effectively suppress the establishment and growth of surgically implanted protoscoleces (Rau and Tanner, 1973). It is possible that moose may exhibit a similar response.

There is some controversy in the literature as to the effects of hydatid infections on the moose host. Addison et al. (1979) reported no apparent relationship between physical condition of the moose and intensity of pulmonary cysts. Based on the above, they concluded that E. granulosus infections are essentially nonpathogenic in the moose. These findings support the views of Rausch, (1952), Ritcey and Edwards (1958) and Rausch (1959). Many workers, however, have concluded that hydatid cysts do have a debilitating effect on the intermediate host. Since the transmission of this cestode is accomplished by the ingestion of the intermediate host by the definitive host, it would be "advantageous" for the parasite to debilitate the cervid host in such a manner that its chances of being eaten by the canid host are increased (Holmes and Bethel, 1972; Kennedy, 1975). Cowan (1951) suggested that heavy hydatid infections in elk might reduce the animal's ability to survive adverse conditions. Similarly, Crisler (1956) provided circumstantial evidence that large numbers of hydatid cysts in the lungs predispose caribou to predation by wolves. Several authors (Harper et al., 1955; Mech, 1970; Peterson, 1977; Allen,

1979) suggested that heavy pulmonary infections of _E. granulosus_ might impair a moose's ability to survive by rendering it more vulnerable to predation and other environmental pressures.

The role of _E. granulosus_ in moose-wolf interactions is probably related to the wolves' keen sensitivity to the condition of their prey. A moose harbouring a heavy pulmonary infection may exhibit some type of behavioural pathology, however slight, which would indicate to the wolves that it was easy prey. Mech (1970) stated that, "probably their (hydatid cysts') main effect on a moose is in interfering with its breathing, for large numbers of cysts may replace a great percentage of lung tissue. Perhaps this would cause little harm to an animal not forced to exert itself, but to an individual that must run from wolves or stop to fend them off, the condition would have dire consequences".

There is some circumstantial field evidence to support the hypothesis that _E. granulosus_ infections in moose induce susceptibility to predation or other stressful environmental conditions. In Ontario, Peterson (1955) examined a fresh, wolf-killed moose carcass and described the lungs as being "so completely filled with hydatid cysts that it seemed incredible that they could have functioned sufficiently to keep the animal alive during normal activity, much less to ward off an attack by timber wolves". Ritcey and Edwards (1958) reported the sudden death, under stressful conditions, of a young cow moose which harboured numerous pulmonary cysts. However, these authors did not relate the death of this moose to her being infected with _E. granulosus_. On Isle Royale, Allen (1979) examined the remains of four wolf-killed moose (viscera intact) and found heavy hydatid infections in all of them.

Rau and Caron (1979) studied the susceptibility of infected moose to hunting and suggested that heavy pulmonary burdens of _E. granulosus_ cysts may affect the moose host by increasing its chances of being shot by hunters.

Previous studies on _E. granulosus_ infections in moose (Samuel et al., 1976; Addison et al., 1979; Rau and Caron, 1979) have reported mainly on prevalence and intensity and have correlated these parameters with age. The present study explores more fully the prevalence, abundance, mean intensity and biomass of infection at the individual and population levels. By examining these parameters in relation to variables such as age and sex of the host, the distribution of _E. granulosus_ in the moose population of southwestern Quebec is described. The relationships between cyst weight and intensity, and the correlation of these parameters with age, are examined. Viability of protoscoleces produced by the hydatid cysts and host response in the form of cyst-cyst interaction are also investigated. These data may provide an insight into the aquisition and growth of pulmonary cysts as well as to the possible effects of such infections on the moose host.

B. MATERIALS AND METHODS

1. Field Methods

The lungs examined during the course of this study were obtained from moose shot during annual fall hunts (Appendix 3-1) in the Rouge-Matawin, La Verendrye and Mastigouche Reserves. These hunts are strictly controlled by the MLCP and are conducted in specified hunting zones (Appendices 3-2 to 3-5) for a limited time, usually four days. Hunters are selected and assigned to their zones and time slots by lottery. The groups consist of two hunters and a guide or (most often) three hunters. Each group is permitted to shoot one moose. Prior to each hunting session, the hunters are asked to collect the lungs if they kill a moose. This is done during a personal interview or by handing out a letter (Appendix 3-6). The hunters are then furnished with a kit which includes a diagram illustrating the life cycle of E. granulosus (Appendix 3-7), a bag to collect the lungs and various maps and regulations of the MLCP. The hunters are instructed to give the lungs to the park biologist when registering their kill. At this time, the two middle incisor teeth of the moose are extracted and used later in determining the age of these animals. During the 1979 and 1980 hunts in the Rouge-Matawin Reserve, each party was interviewed upon the completion of a successful hunt. The majority of the lungs collected during the hunts was frozen prior to examination. However, in 1981, it was possible to examine a number of fresh lungs from the La Verendrye and Rouge-Matawin Reserves. Some of the lungs were missing one or more lobes, or had sustained considerable damage from bullets. Such lungs were not included in the analyses. Data from moose shot in the Rouge-Matawin Reserve (1978, 1979) were supplied by Dr. M. E. Rau, McGill University.

To determine if infected moose react differently to hunters than do uninfected moose, all successful hunters were interviewed about the behaviour of the moose prior to its being shot. Their assessment of a moose's behaviour was compared to known levels of infection in these animals.

2. Laboratory Methods

Moose lungs range in weight from approximately 4.2 kilograms for a calf to 8.3 to 10.5 kilograms for an adult (Figure 3-1). in comparison, macroscopic cysts ranged from 0.1 grams (about one millimeter in diameter), to 20 to 30 grams (about four or five centimeters in diameter). To facilitate location of the very small cysts, the lungs were cut into thin (approximately one centimeter) slabs of tissue and palpated. This method is comparable to that used by Addison et al., (1979) and by Rau and Caron (1979). Loose host tissue was removed from the excised cysts (Figure 3-2) and the weight of each was recorded in grams to one decimal place using a Mettler digital balance. Site of cyst (left or right lung) was recorded for all 1981 data and for the 1980 sample from La Verendrye. Using the I1 incisor teeth collected during the hunt, the moose were aged according to the method of Ouellet (1977). These data were supplied by the MLCP.

Figure 3-1. Lungs of an adult moose.
(Bar represents 15 centimeters.)

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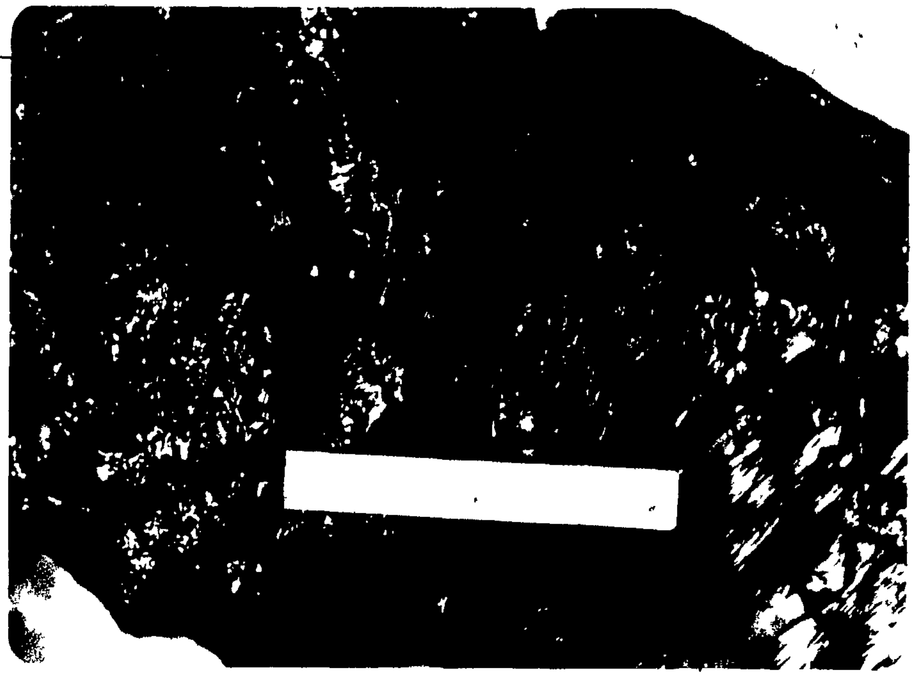
Figure 3-2. _Echinococcus granulosus_ infections in the moose.

A. Moose lung infected with the hydatid cysts of _Echinococcus granulosus_.

B. Excised cysts with loose host tissue removed.

A



B

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Viability of protoscoleces was determined for a sample of cysts from fresh lungs. Anderson and Loveless (1978) reported that protoscoleces of E. granulosus survive for 16 days at one to ten degrees centigrade. In view of these results, and to ensure a reliable estimate of protoscolex viability, only lungs from moose that had been dead less than five days, when the ambient temperature was within the above-mentioned range, were used. Protoscoleces were considered viable if active hook and body movements were observed (Batham, 1957; Schwabe et al., 1963; Anderson and Loveless, 1978). The number of viable protoscoleces in the first 100 examined from each cyst was used to determine percent viability. Five cysts from each of 18 moose were examined in this manner.

3. Analysis of Data

In all statistical tests, the level of significance was set at five percent. Prevalence, mean intensity, abundance, mean cyst weight and total biomass of infection were determined for all moose in the sample. The Chi-square test of independence (Siegel, 1956) was employed to test fluctuations in prevalence. Differences among the other above-mentioned parameters and variables such as age, sex and site of infection were tested by one-way analysis of variance (Sokal and Rohlf, 1982) and Duncan's new multiple range test (Siegel, 1956). With the exception of prevalence, and of mean intensity between male and female moose, the samples proved to be homogeneous with respect to the above parameters and variables. Therefore, these data were pooled for further analyses.

The relationships between moose age and the abundance, mean intensity, cyst weight and total biomass were examined and the significance of any observed correlations were tested using the Pearson product moment correlation coefficient (r) (Sokal and Rohlf, 1982) or the Spearman rank correlation coefficient (r_s) with corrections for ties (Siegel, 1956).

The force of infection, λ, is defined as the instantaneous rate of infection per host per unit time (Anderson and May, 1979) and may be used to estimate the rate of infection when the actual number of available infective stages is not known. By examining the proportion of uninfected moose in each age group, the force of infection and the average age of moose at infection (Anderson and May, 1979 and 1982) were estimated.

Cyst growth and possible cyst-cyst interaction within individual moose were examined by comparing the weights of cysts in a particular moose to the rank of these cyst weights.

To test for susceptibility of infected moose to hunting, the Mann-Whitney U test with corrections for ties (Siegel, 1956) was employed to determine if the sequence of moose kills was independent of abundance of infection.

C. RESULTS

Results of the examination of the lungs from 489 moose are presented in this chapter. This total represents data from seven samples (i.e. four, two and one years from the Rouge-Matawin, La Vérendrye and Mastigouche Reserves respectively) (Table 3-2).

1. General Description of the Moose Sampled from Southwestern Quebec

The overall age distribution of the moose sampled in this study is presented in Figure 3-3. Age distributions in the individual reserves are similar to that of the total sample (Appendix 3-8). The average age of moose shot during the annual hunts ranges from 3.7 years (Rouge-Matawin, 1981) to 5.5 years (Rouge-Matawin, 1978) with an overall mean age of 4.4 years (Table 3-3). None of the mean ages differed significantly between reserves or among years ($F=1.18$, $p > 0.10$).

A greater proportion of males (63%) than females (38%) is represented in this sample of hunter-killed moose. The mean age of female moose (4.8 years) is significantly higher than that of the males (4.2 years) ($F=4.86$, $p < 0.05$).

2. Homogeneity Between Reserves and Among Years

Abundance, mean intensity, mean cyst weight and biomass of infection did not vary significantly among the seven samples ($F = 0.72$,

Table 3-2. Numbers of moose sampled during the annual hunts in the Rouge-Matawin, La Verendrye and Mastigouche Reserves.

YEAR	RESERVE			TOTAL
	Rouge-Matawin	La Verendrye	Mastigouche	
1978	45			45
1979	54			54
1980	46	137		183
1981	42	122	43	207
Total	187	259	43	489

Figure 3-3. Age distribution of the moose shot during the annual hunts (1978 to 1981) in all three study areas (the Rouge-Matawin, La Verendrye and Mastigouche Reserves).

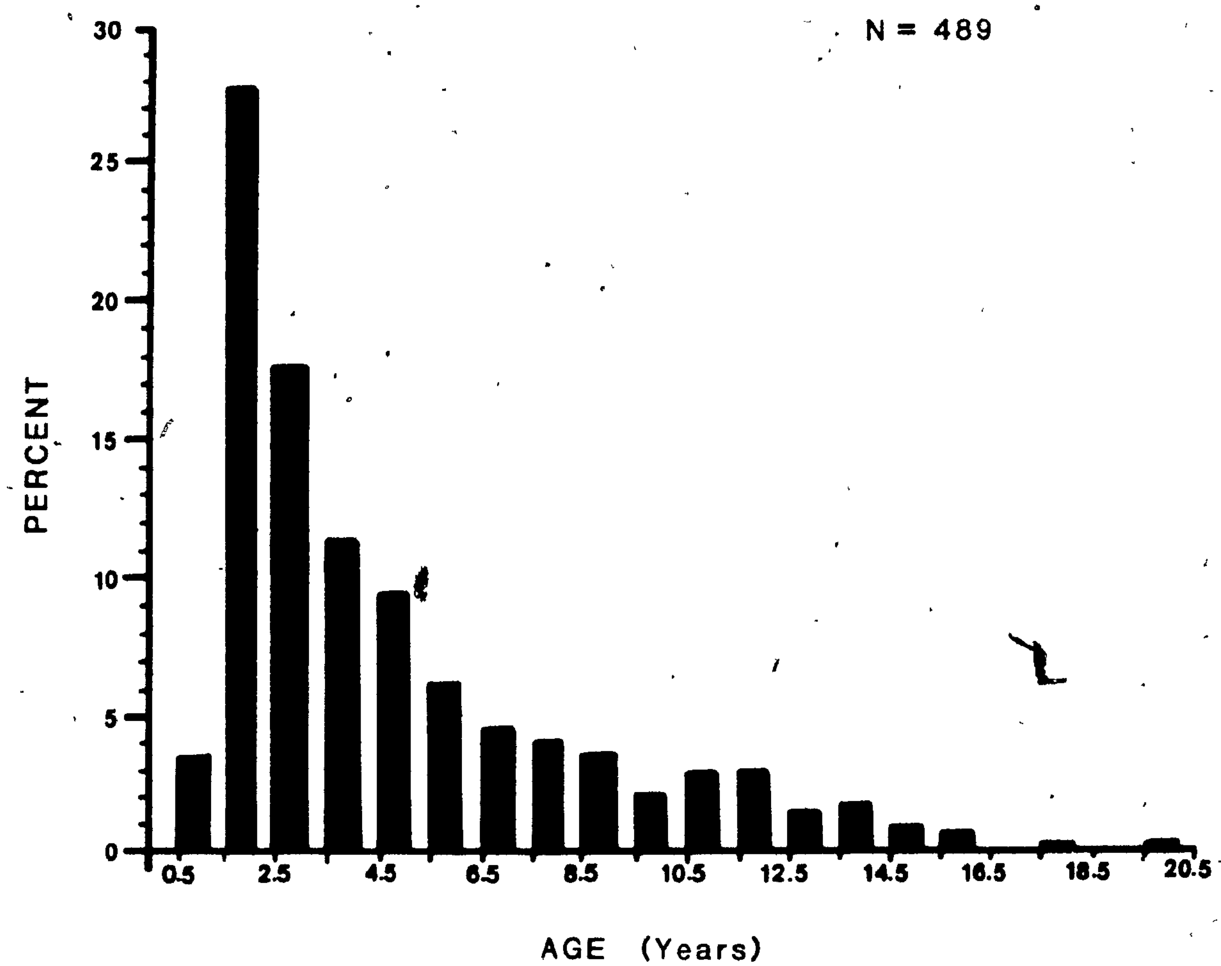

N = 489
PERCENT
30
25
20
15
10
5
0
0.5
2.5
4.5
6.5
8.5
10.5
12.5
14.5
16.5
18.5
20.5
AGE (Years)

Table 3-3. Mean age of moose sampled during the annual hunts in the Rouge-Matawin, La Verendrye and Mastigouche Reserves.

YEAR	RESERVE			
	Rouge-Matawin	La Verendrye	Mastigouche	Mean Age per year
1978	5.5 (0.57) n=45			5.5 (0.57) n=45
1979	4.6 (0.48) n=54			4.6 (0.48) n=54
1980	4.3 (0.42) n=46	4.3 (0.30) n=137		4.4 (0.25) n=183
1981	3.7 (0.47) n=42	4.1 (0.32) n=122	4.7 (0.59) n=43	4.1 (0.24) n=207
Mean age per reserve	4.6 (0.25) n=187	4.2 (0.22) n=259	4.7 (0.59) n=43	4.4 (0.16) n=489

( ) Numbers in brackets represent one standard error.

0.92, 0.92 and 1.86 respectively, $p > 0.10$ in all cases). Figures 3-4, 3-5, 3-6 and 3-7 present the means and $\pm$ 95 percent confidence limits for the above four parameters. The calculated values for abundance, mean intensity, mean cyst weight and biomass are summarized in Appendix 3-9. Prevalence of infection did vary significantly when tested over all seven samples (X^2=18.71, df=6, $p < 0.01$). Due to these results, prevalence is considered separately and the other parameters are analysed using the pooled (n=489) data.

3. Prevalence of Infection with Echinococcus granulosus

The observed differences in prevalence from one sample to another are due to variation among years (X^2=14.27, df=3, $0.25 < p < 0.05$) and not to differences between reserves (X^2=2.99, df=2, $p > 0.10$)(Figure 3-8).

Prevalence increases with age; rising quickly among younger moose and reaching a plateau of approximately 100% among older individuals (Figure 3-9). Moose reach maturity at between five and six years of age (Peterson, 1974) and therefore, it may be said that virtually all older moose are infected. To further examine this relationship, the prevalence of infection in "young" and "mature" moose is considered separately. It may be seen from Figure 3-10 that prevalence is relatively constant in the younger moose (X^2=12.29, df=6, $p > 0.05$) but is subject to significant annual fluctuation among the older, more heavily infected individuals.

Figure 3-4. 95 Percent confidence limits for abundance of *Echinococcus granulosus* in moose shot during the annual hunts in the three study areas.

(Overlapping bars indicate no significant differences.)

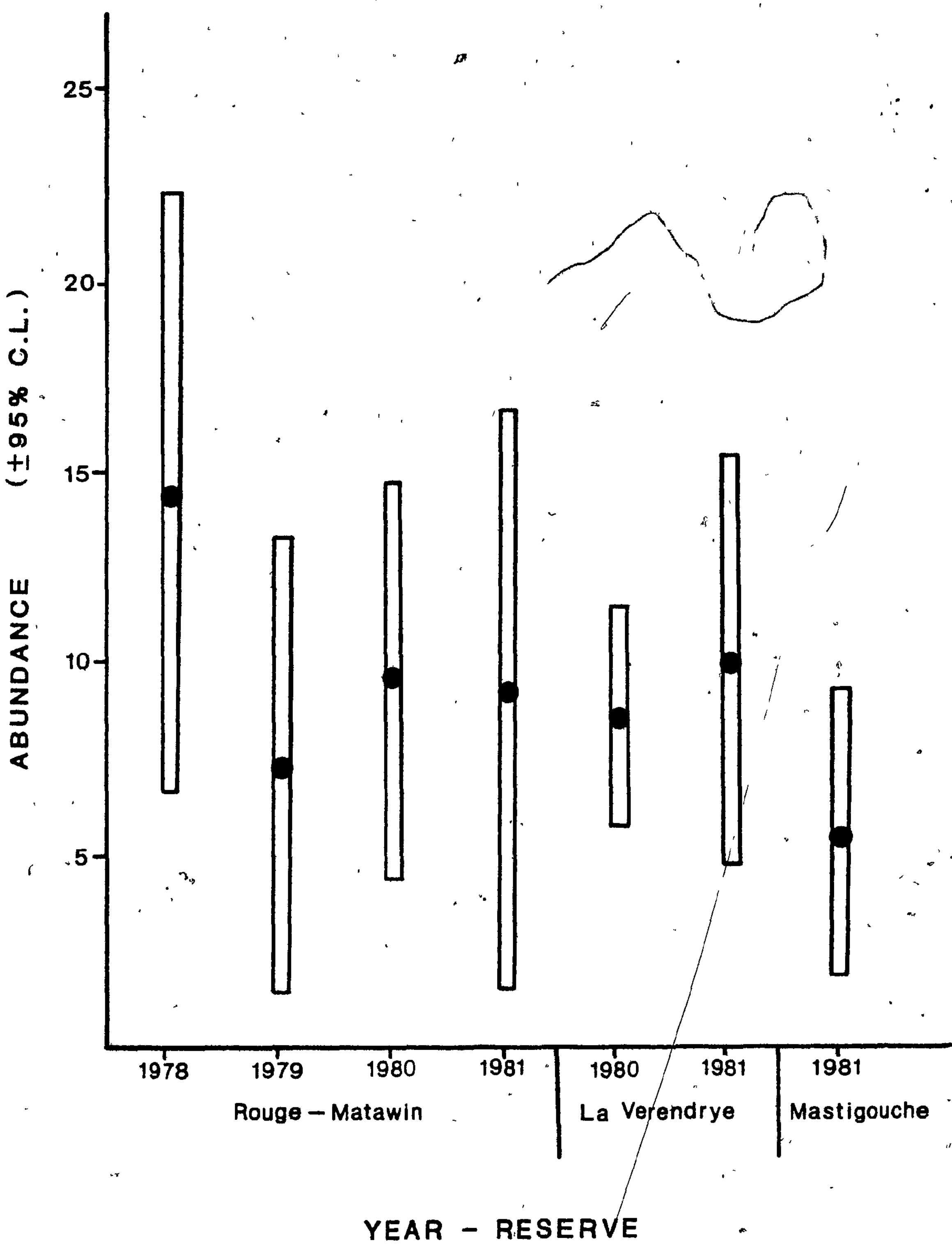
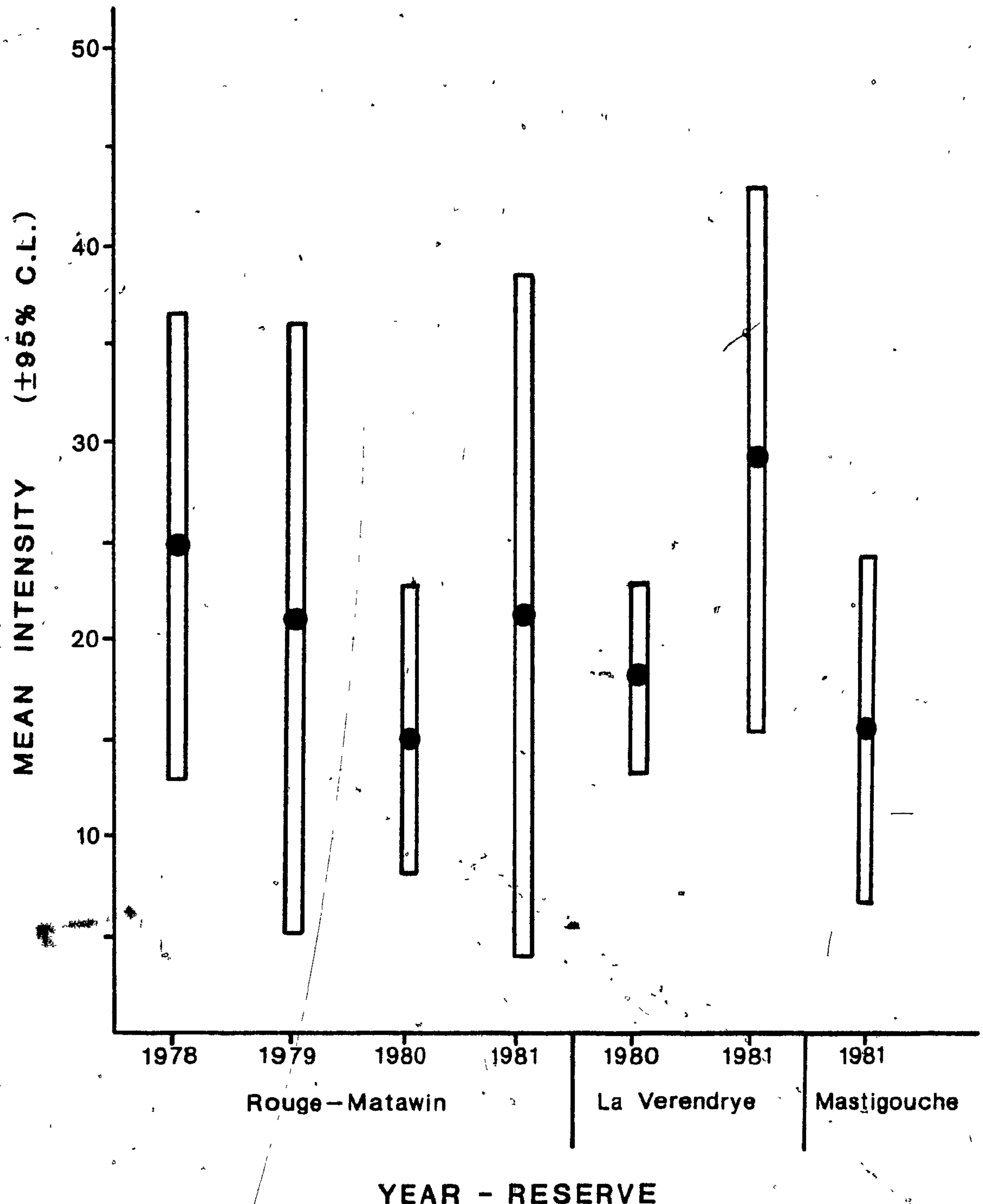

25
20
15
10
5
ABUNDANCE (±95% C.L.)
1978
1979
1980
1981
1980
1981
1981
Rouge – Matawin
La Verendrye
Mastigouche
YEAR – RESERVE

Figure 3-5. 95 Percent confidence limits for mean intensity of *Echinococcus granulosus* in moose shot during the annual hunts in the three study areas.

(Overlapping bars indicate no significant differences.)



MEAN INTENSITY (±95% C.L.)
50
40
30
20
10
1978
1979
1980
1981
1980
1981
1981
Rouge-Matawin
La Verendrye
Mastigouche
YEAR - RESERVE

Figure 3-6. 95 Percent confidence limits for mean cyst weight of Echinococcus granulosus cysts in moose shot during the annual hunts in the three study areas.

(Overlapping bars indicate no significant differences.)

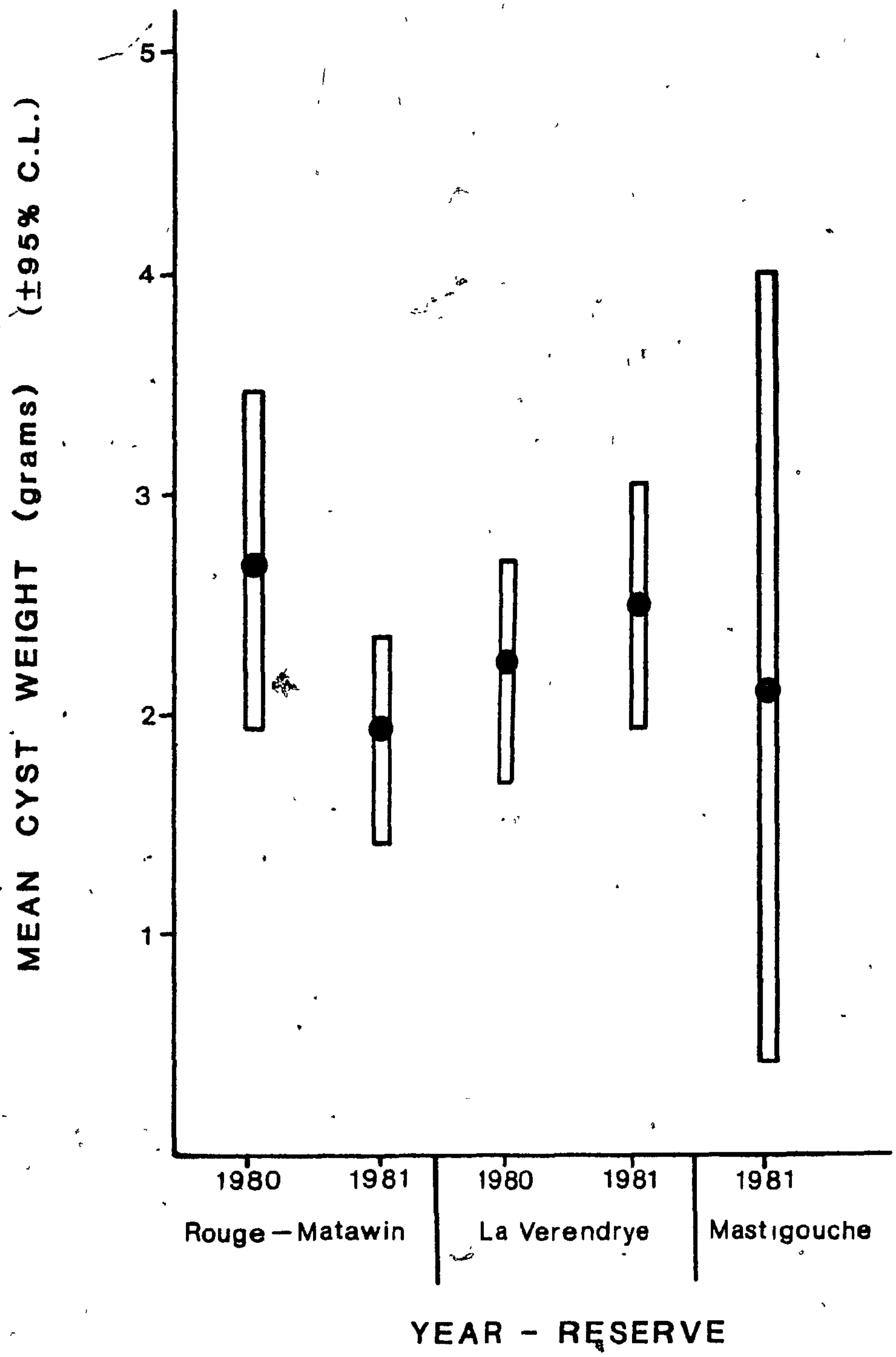

MEAN CYST WEIGHT (grams) (±95% C.L.)
5
4
3
2
1
1980
1981
1980
1981
1981
Rouge—Matawin
La Verendrye
Mastigouche
YEAR - RESERVE

Figure 3-7. 95 Percent confidence limits for biomass of <u>Echinococcus granulosus</u> cysts in moose shot during the annual hunts in the three study areas.

(Overlapping bars indicate no significant differences.)

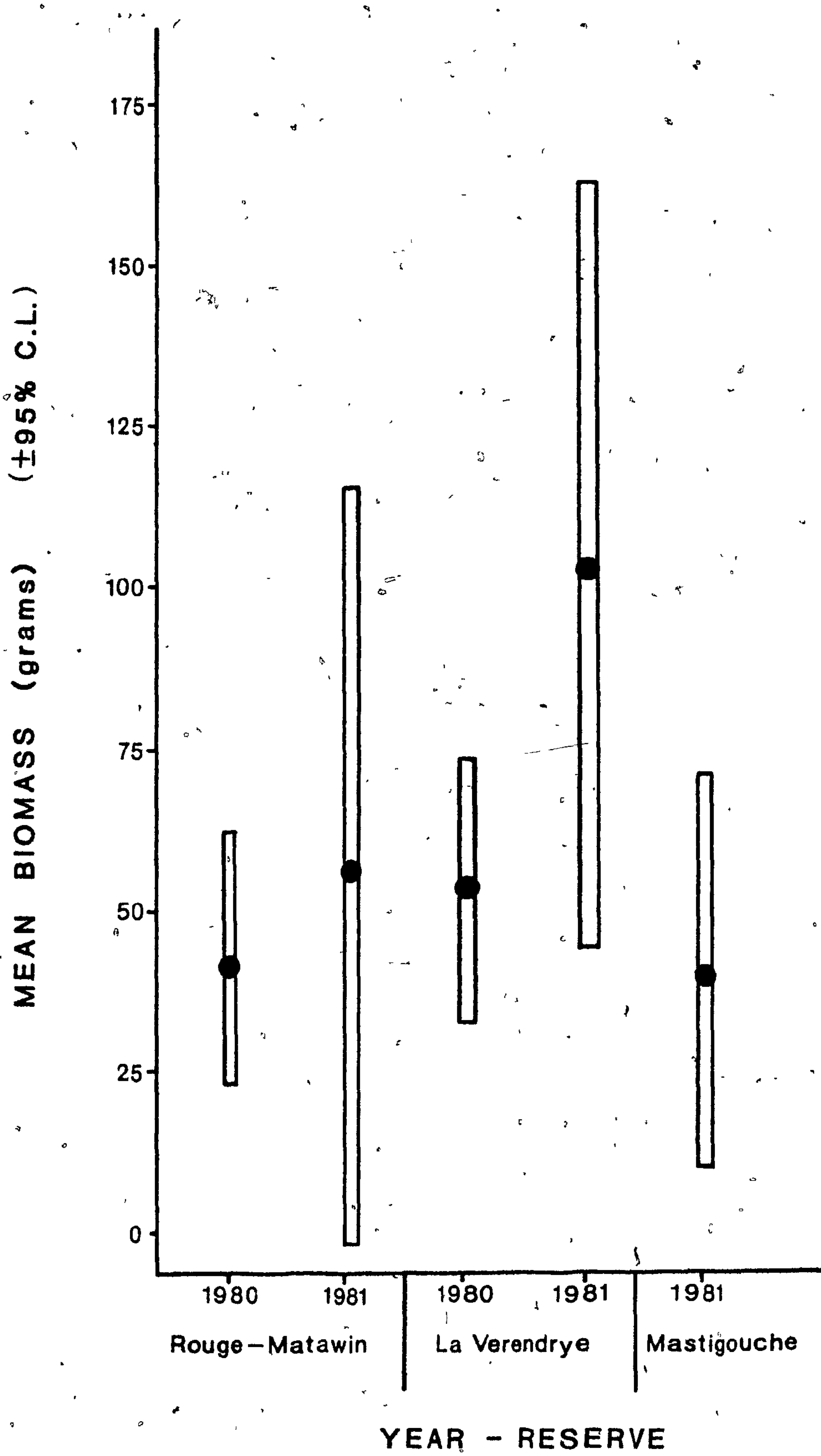
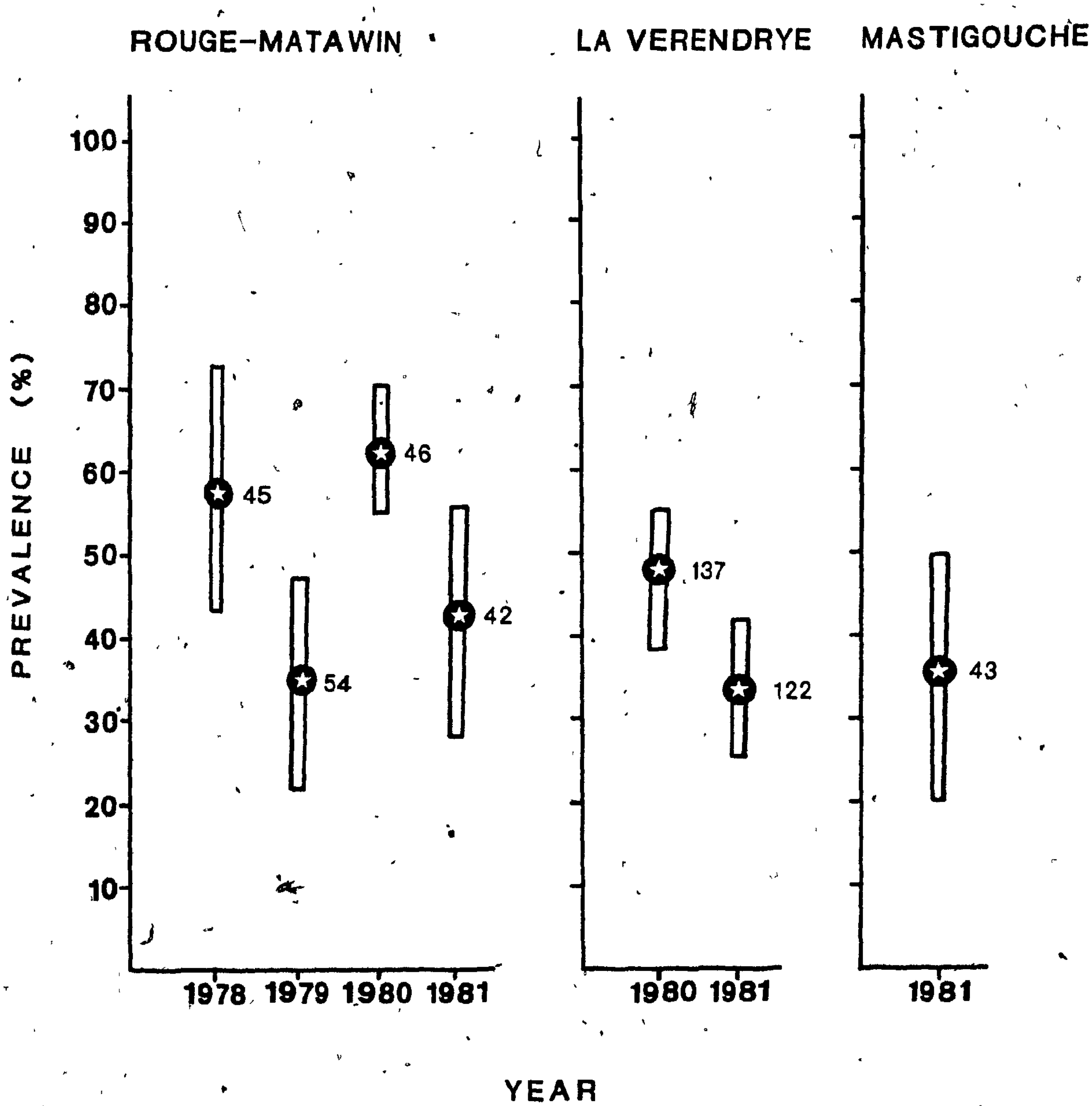

MEAN BIOMASS (grams) (±95% C.L.)
175
150
125
100
75
50
25
0
1980
1981
1980
1981
1981
Rouge–Matawin
La Verendrye
Mastigouche
YEAR - RESERVE

Figure 3-8. Annual fluctuations in prevalence (%) among moose from the three study areas.

Numbers beside prevalence dots indicate sample size.

Bars represent ± 95% confidence limits.

(Overlapping bars indicate no significant differences.)



ROUGE-MATAWIN
LA VERENDRYE
MASTIGOUCHE
PREVALENCE (%)
100
90
80
70
60
50
40
30
20
10
45
54
46
42
137
122
43
1978 1979 1980 1981
1980 1981
1981
YEAR

Figure 3-9. Age-prevalence curve for moose infected with <u>Echinococcus granulosus</u>.

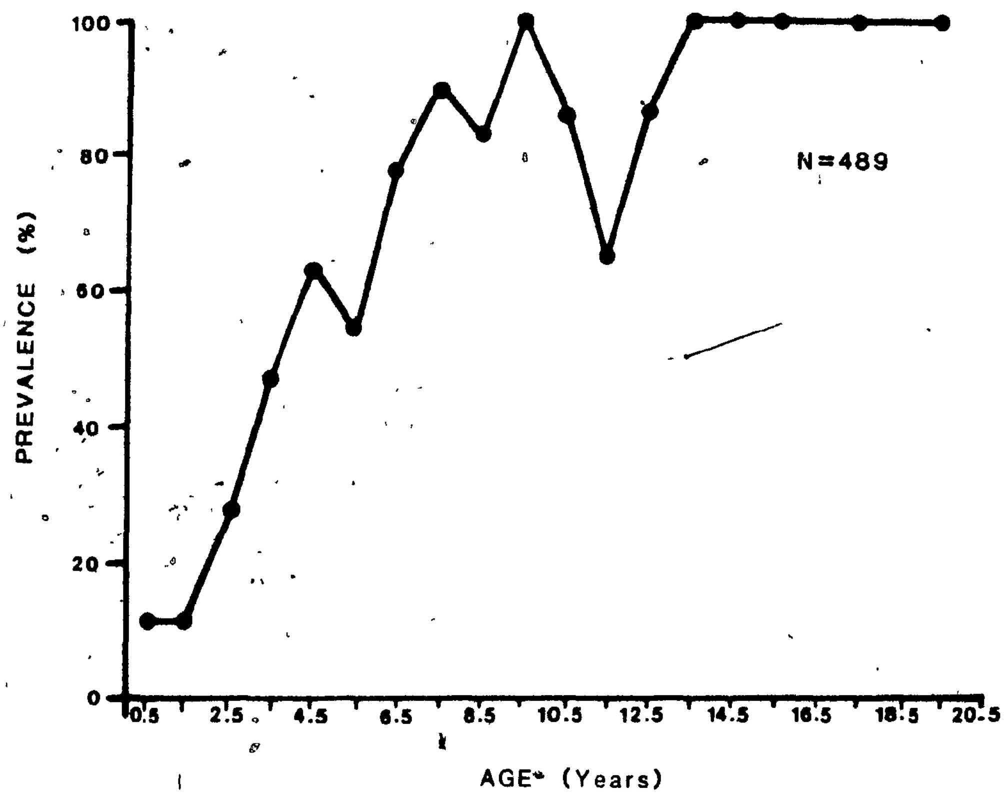
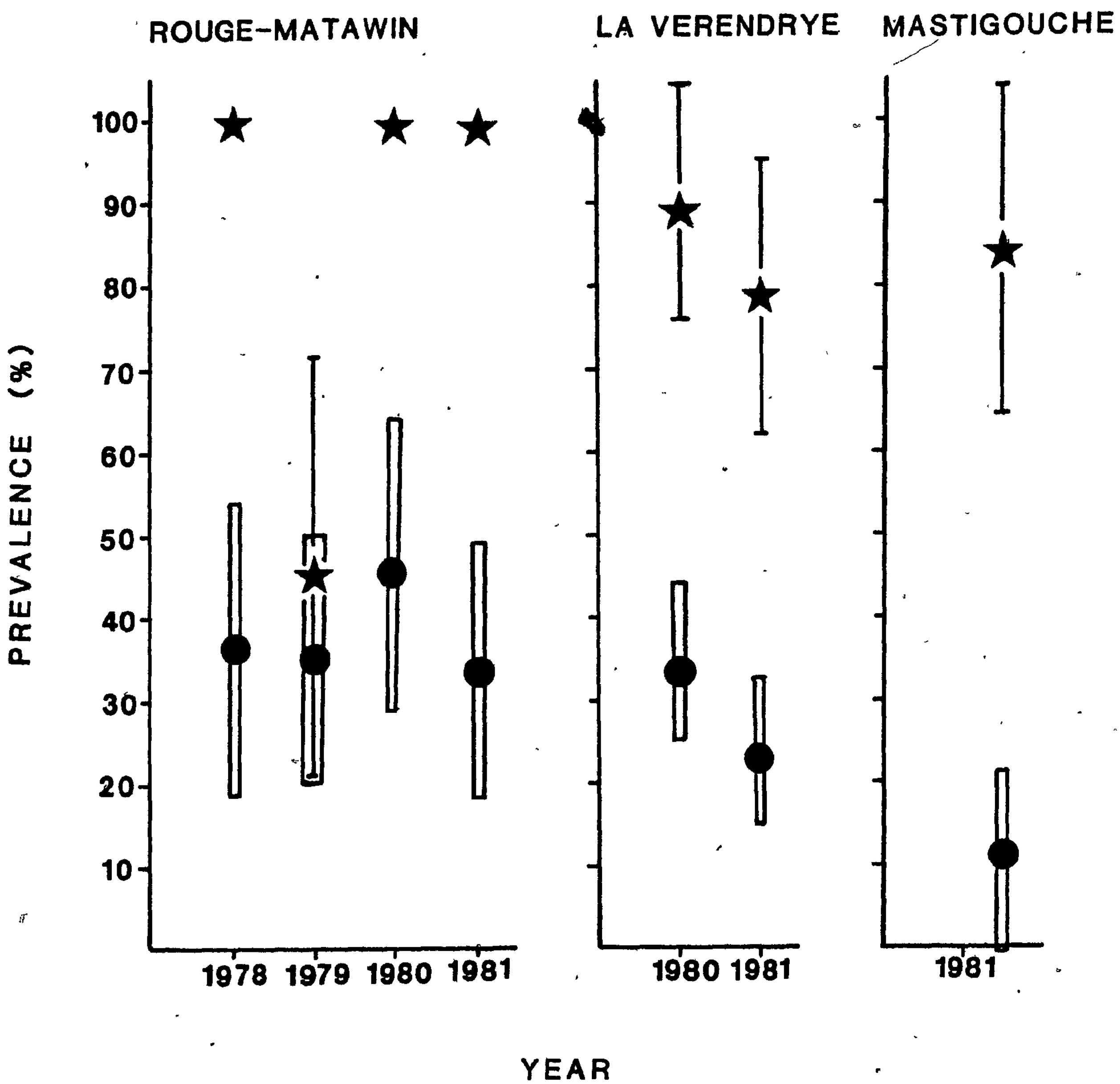

100
80
60
40
20
0
PREVALENCE (%)
N=489
0.5
2.5
4.5
6.5
8.5
10.5
12.5
14.5
16.5
18.5
20.5
AGE (Years)

Figure 3-10. Annual fluctuations in prevalence (%) among "young" and "mature" moose in the three study areas.

★ Prevalence and ± 95% confidence limits for moose > 5.5 years.

● Prevalence and ± 95% confidence limits for moose ≤ 5.5 years.

(Overlapping bars indicate no significant differences.)



ROUGE-MATAWIN
LA VERENDRYE
MASTIGOUCHE
PREVALENCE (%)
100
90
80
70
60
50
40
30
20
10
1978
1979
1980
1981
1980
1981
1981
YEAR

No significant differences in prevalence were detected between males and females ($X^2=0.36$, df=1, $p>0.99$) or between infections in the left and right lungs ($X^2=0.21$, df=1, $p>0.99$).

4. Comparison of Infection Parameters of Echinococcus granulosus in Male and Female Moose

After testing for differences in site, abundance, mean intensity, mean cyst weight and total biomass of infection, only mean intensity was shown to differ significantly between males and females (18.0 and 25.4 cysts respectively) ($p<0.05$).

5. Pattern of Infection of Echinococcus granulosus in the Moose Population

a) Overdispersion of Echinococcus granulosus in the Moose Population

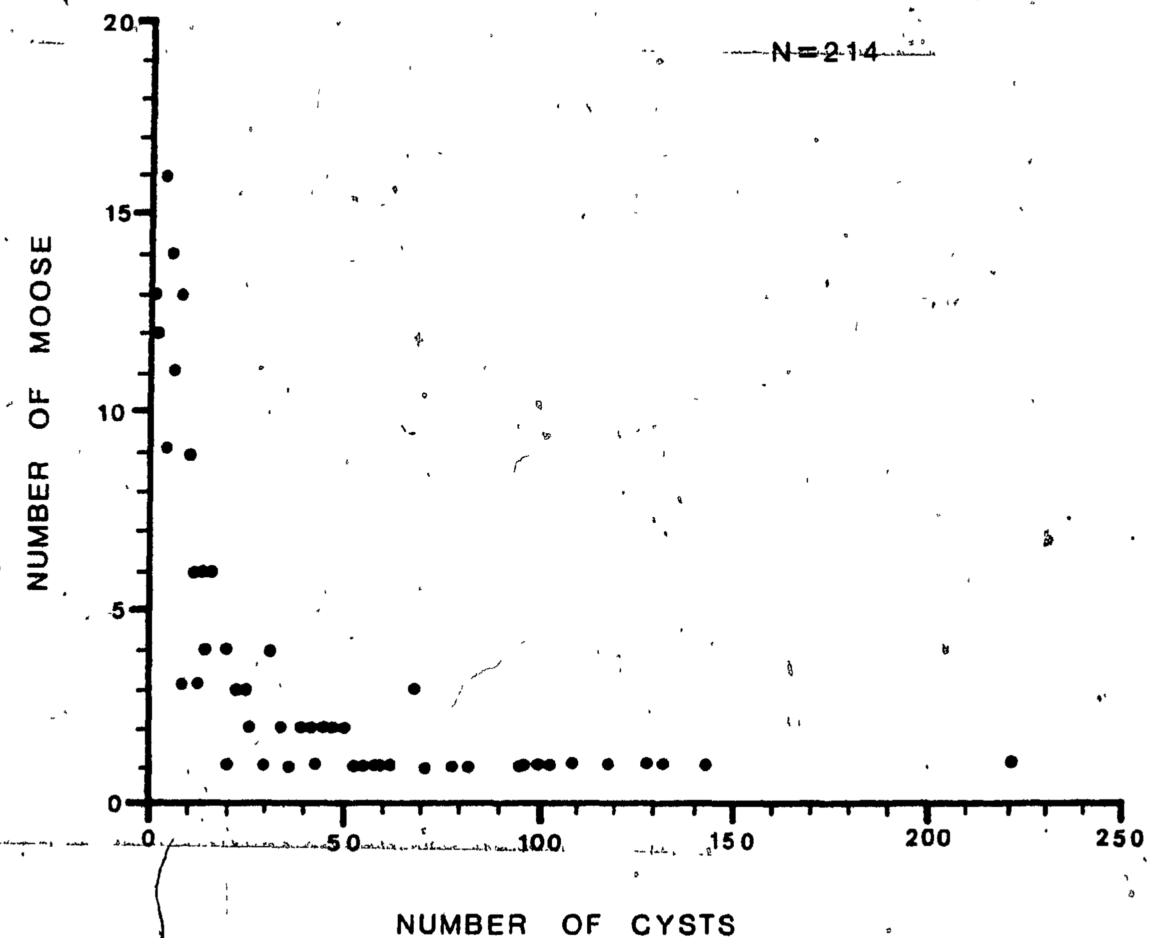
The variance to mean ratio, which is considered to be a measure of over-dispersion (Anderson, 1978), was calculated for abundance. This ratio ($s^2/\bar{x}=54.5$) indicates that E. granulosus is very overdispersed in the moose population (Figure 3-11).

b) Force of Infection and Average Age at Infection

Following the assumptions that E. granulosus does not cause direct mortality in the moose and that moose do not lose this infection, the

Figure 3-11. Overdispersion of Echinococcus granulosus in the moose population.

(Total sample = 214 infected moose + 275 uninfected moose.)


N=214
NUMBER OF MOOSE
0
5
10
15
20
0
50
100
150
200
250
NUMBER OF CYSTS

force of infection, λ, is estimated to be 0.2/moose/year. The average age at which moose become infected, $1/\lambda$, (Anderson and May, 1982) is 5.0 years.

c) Correlation of Infection Parameters with Moose Age

Table 3-4 presents the Spearman rank correlation coefficients (r_s) and 95 percent confidence limits for the correlation of abundance; mean intensity; mean, maximum, and minimum cyst weight; and biomass with moose age. All except minimum cyst weight are positively correlated with age ($p < 0.0001$). Minimum cyst weight, however, remains relatively constant as the moose grow older ($r_s=0.174$, $p > 0.10$).

6. Cyst-Cyst Interaction and Protoscolex viability

The relationship between cyst weight and the rank of these weights in a number of individual moose may be seen in Figure 3-12. The distribution of cyst weights exhibits a distinctive pattern. It appears that a few cysts in each infection attain a relatively large size whereas the majority of cysts remain fairly small.

The examination of protoscoleces from within the cysts revealed that 69 to 95 percent (overall mean 86 percent) of larval E. granulosus from moose in the La Verendrye Reserve are viable.

Table 3-4. Spearman's correlation coefficients (r_s) for the correlation of infection parameters with moose age.

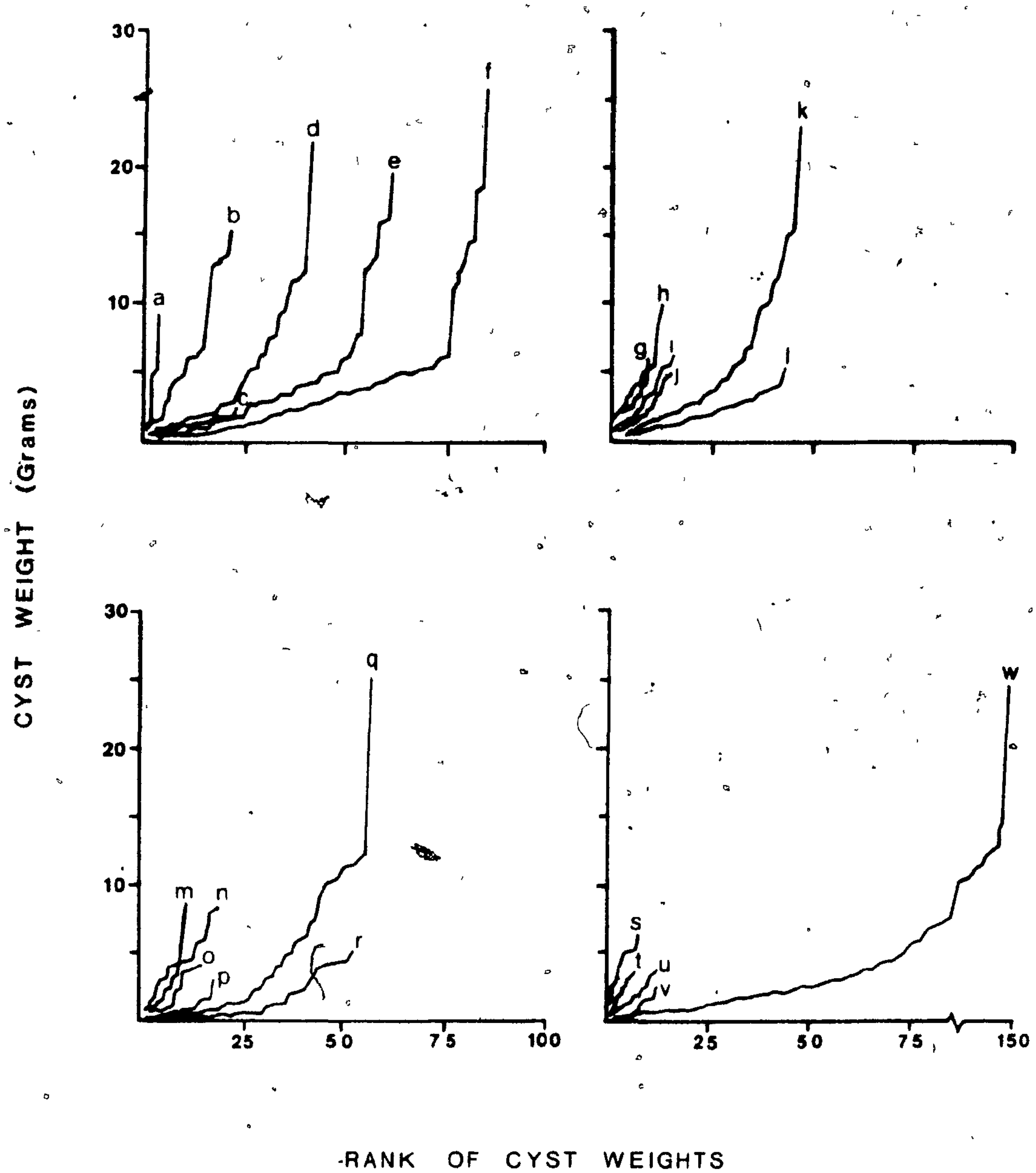
Parameter	n	r_s	95% Confidence limits
Abundance	489	0.624**	0.566 - 0.675
Mean intensity	214	0.506**	0.399 - 0.599
Mean cyst weight	169	0.517**	0.401 - 0.616
Max. cyst weight	169	0.616**	0.512 - 0.702
Min. cyst weight	169	0.105	0.046 - 0.252
Biomass	169	0.615**	0.511 - 0.701

** $p < 0.0001$

Figure 3-12. The relationship between cyst weight and the rank of cyst weights for 23 moose (a - w) from the La Verendrye Reserve (1981).

Legend:

Moose	Age
a	11.5
b	10.5
c	3.5
d	10.5
e	13.5
f	9.5
g	9.5
h	12.5
i	4.5
j	12.5
k	10.5
l	4.5
m	13.5
n	8.5
o	7.5
p	4.5
q	6.5
r	2.5
s	7.5
t	3.5
u	3.5
v	2.5
w	14.5


CYST WEIGHT (Grams)
30
20
10
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s
t
u
v
w
25
50
75
100
150
RANK OF CYST WEIGHTS

7. Susceptibility of Infected Moose to Hunting

a) Results of Hunter Interviews

Sixty-two percent of the hunters interviewed (Rouge-Matawin, 1979 and 1980) reported that the moose had seen them before they fired at it. Of these hunters, only one group (2 percent) noted an abnormal behaviour of the moose. This animal had taken no evasive action when confronted by two of the hunters. The lungs of this moose were heavily infected (108 cysts). Other than advanced age, the hunters had not noted any obvious malcondition of the moose.

b) Sequence of Kill Analysis

Except for the 1978 sample from Rouge-Matawin, the Mann-Whitney U test revealed that the sequence of moose kills is independent of abundance of infection. Values of the test statistic (z) for the samples from the Rouge-Matawin, La Verendrye and Mastigouche Reserves are presented in Table 3-5.

D. DISCUSSION

1. Age and Sex Distribution of Moose Sampled in Southwestern Quebec

The overall age distribution of moose in the sample is characteristic of a steadily hunted population. It is not biased towards older moose as samples from infrequently or lightly hunted populations are apt to be (Addison and Timmerman, 1974; Cumming, 1974).

Table 3-5. Results of Mann-Whitney U tests for the sequence of kill analysis.

SAMPLE		ABUNDANCE		TEST STATISTIC (z)
Reserve	Year	First 25% of moose shot	Remaining 75% of moose shot	
Rouge-Matawin	1978	30.9	9.0	2.404 **
	1979	12.7	5.6	0.341
	1980	5.6	10.8	1.124
	1981	6.6	9.8	0.016
La Verendrye	1980	6.6	9.3	0.004
	1981	16.1	7.9	0.004
Mastigouche	1981	3.3	6.3	0.526

** $p < 0.0073$

Simkin (1965) assumes that nearly equal numbers of male and female moose are born, and that nearly equal numbers of each sex occur in a natural population. Pimlott (1959) and Peterson (1977) show data which support these assumptions. Thus, the greater proportion of males in the sample may be indicative of a hunter bias towards bulls rather than a reflection of the true sex ratio in the moose population (Cumming, 1974). Furthermore, selective hunting of males is facilitated by the fact that moose hunting seasons coincide with the rut (mating season), during which time the bulls are more aggressive and therefore, more frequently encountered (Crête et al., 1981). Young, unmated males are especially belligerent and responsive to hunters' calls (F. Messier and M. Crête, unpublished data). This may serve to lower the mean age of males in the sample which may in turn account for the lower intensity of E. granulosus infections observed in males, since the younger moose are less heavily infected than are the older individuals.

2. Echinococcus granulosus Infections in Moose from Southwestern Quebec.

The absence of significant differences between infection parameters of all seven samples, coupled with the fact that prevalence varies from year to year but not between reserves, indicates that the moose sampled in this study are taken from a homogeneous population in which the prevalence of E. granulosus infections undergoes annual fluctuations. Since moose do not lose this infection, the most likely cause of a decline in prevalence is the removal of infected individuals. Conversely, to increase the prevalence, infected moose must be added to the population at a faster rate than they are removed. If a constant force of infection of 0.2/moose/year is assumed, the variation in the prevalence of E. granulosus in the moose population of southwestern Quebec may be due to changes in the rate of removal of heavily infected animals. Many factors, acting alone or in concert, have been shown to influence this rate. Predation and hunting pressure may be affected by environmental conditions such as winter severity (Coady, 1974; Peterson and Allen, 1974; Franzman, 1978), food supply (Peek, 1974; Allen, 1979) and habitat changes (fire, logging, etc.) (Peterson, 1955; Krefting, 1974). If indeed the infected moose are more susceptible to predation, slight changes in these conditions may influence the rate of removal of heavily parasitized individuals. An increased susceptibility due to higher intensity of E. granulosus infections may also account for the more pronounced fluctuation in prevalence among the older moose, as these are the ones which consistently harbour a greater burden of hydatid cysts.

3. Overdispersion of Echinococcus granulosus in the Moose Population

Overdispersion of a parasite species within the host population has been well documented (Schmid and Robinson, 1972; Anderson, 1978). The distribution of E. granulosus in the moose population of southwestern Quebec follows this pattern, which may be described by the negative binomial model. Crofton (1971) states that, among other factors, overdispersion may result from: non-random distribution of infective stages in the environment; a series of random exposures to infection; and an unequal chance of infection resulting from host variation. Wolves tend to defecate within the immediate vicinity of a kill or along defined trails, a habit which may generate a non-random distribution of E. granulosus eggs in the environment. However, factors which contribute to egg dispersal may diffuse this pattern. Moose tend to occupy a loosely-defined home range (four to five square kilometers) (Krefting, 1974). Consequently, exposure to infection may, to some extent, depend on the location of these ranges in relation to wolf territories, and (or) on the occurrence of wolf-kills in these areas.

4. Cyst-Cyst Interaction

Kennedy (1975) states that the level of infection and successful development of the cystic stage of cestodes is determined by the intermediate host response. He further states that sheep are never able to develop complete immunity to E. granulosus although fewer cysts establish and the host response is stronger in subsequent infections. It has been shown experimentally (Rau and Tanner, 1973) that, in cotton rats, preexisting cysts of E. multilocularis suppress the establishment and growth of subsequent challenge infections. This study presents circumstantial evidence that moose may exhibit a somewhat similar response. Although intensity increases with age, a disproportionately large number of small cysts are found in older moose. This suggests that there may be intra-specific competition wherein subsequently acquired cysts are suppressed by a preexisting infection.

5. Susceptibility of Infected Moose to Predation and Hunting

It has generally been hypothesised that *E. granulosus* may affect the behaviour of stressed moose (Mech, 1970; Peterson, 1977; Allen, 1979; Rau and Caron, 1979). However, no studies have been conducted on the pathologic effects of hydatid infections in this host. Smyth and Heath (1970) and Sun (1982) describe the ~~effects~~ common clinical symptoms of echinococcosis in humans as shortness of breath, chest pain, fever, cough, dyspnea, hemoptysis anaphylactic pneumonia and other secondary lung complications. It is entirely possible that infected moose suffer from similar symptoms. Given the keen awareness of wolves to the condition of their prey (Mech, 1970; Allen, 1979), any of the above pathologic effects may well render infected moose more susceptible to predation. Hunting by humans, on the other hand, is a much more random process. As may be concluded from the post-hunt interviews, there is no "testing" of moose by humans as there is by wolves. Hunters tend to shoot the first moose they see and do so within an average of one minute from the time they first sight the animal. This suggests that the occurrence of infected moose in a sample is reflective of the ratio in which they were encountered by hunters. For all but the 1978 sample from Rouge-Matawin, abundance of infection was independent of sequence of moose-kills. This indicates that, in general, *E. granulosus* infections do not render moose more susceptible to being shot by hunters. However, the pattern of infection in the moose population in certain years may be such that the chances of infected moose being encountered, and therefore shot, by hunters is increased.

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CHAPTER IV. Echinococcus granulosus INFECTIONS IN THE WOLF

A. INTRODUCTION

The wolf is an important predator of ungulates in North America and is thought to be a major factor in the population dynamics of its prey species (Mech, 1970, 1977; Peterson, 1977; Allen, 1979). In Quebec, wolves are the only significant predator of moose (Messier, 1980) and, as such, are necessary in maintaining Echinococcus granulosus infections in the moose population of this province. This view is supported by the fact that E. granulosus does not occur in the moose of Newfoundland in the absence of wolves (Threlfall, 1967), but does occur elsewhere in North America where moose and wolves coexist. Infection of wolves with E. granulosus has been reported from Alaska (Rausch and Williamson, 1959); the Yukon and Northwest Territories (Choquette et al., 1973); Alberta (Cowan, 1948; Holmes and Podesta, 1968); Minnesota (Riley, 1939; Erickson, 1944); Ontario (deVos and Allin, 1949; Freeman et al., 1961); and Quebec (Trudeau, 1981, unpublished report of the Canadian Wildlife Service, Ottawa). Prevalence among adult wolves ranges from 20 percent in Ontario (Freeman et al., 1961) to 72 percent in Alberta (Holmes and Podesta, 1968) (Table 4-1).

Whereas heavy pulmonary infections of E. granulosus are hypothesised to cause behavioral pathology in a stressed intermediate host, (Peterson, 1955; Crisler, 1956; Mech, 1970; Allen, 1979) the adult worm apparently causes little pathology in the definitive host. Medda (1966) reports

Table 4-1. Summary of North American reports of wolves infected with <u>Echinococcus</u> <u>granulosus</u>.

LOCATION	PREVALENCE (%)	Number examined	REFERENCE
Alaska	30	(60/200)	Rausch and Williamson, 1959
Yukon	22	(19/89)	Choquette et al., 1973
N.W.T.	24	(5/21)	Choquette et al., 1973
Alberta	72	(71/98)	Holmes and Podesta, 1968
Minnesota	28	(5/18)	Erickson, 1944
Ontario	20	(103/520)	Freeman et al., 1961
Ontario	62	(36/58)	Sweatman, 1952
Quebec	61	(22/36)	Trudeau, 1981
Quebec	62	(8/13)	present study

that, in the canid, adult E. granulosus cause little more than local inflammation of the small intestine, even though they may be present in very large numbers. Just as it may be "advantageous" for this parasite to debilitate the intermediate host, so it may be "advantageous" for it not to debilitate the definitive host. It may be argued that, from the parasite's point of view, a robust definitive host is a necessity since transmission depends on its (the canid's) success as a predator.

The question which is addressed in this chapter is the following: what levels of prevalence and intensity of E. granulosus in the wolf population are associated with a given level of parasitism in the moose population? None of the above studies on E. granulosus infections in wolves have investigated the prevalence of this parasite in a coexisting moose population. This study estimates the infection levels in wolves from the La Verendrye Reserve. These data are then discussed in light of the observed infection levels in moose from the same study area.

B. MATERIALS AND METHODS

1. Collection and Necropsy of Wolf Carcasses

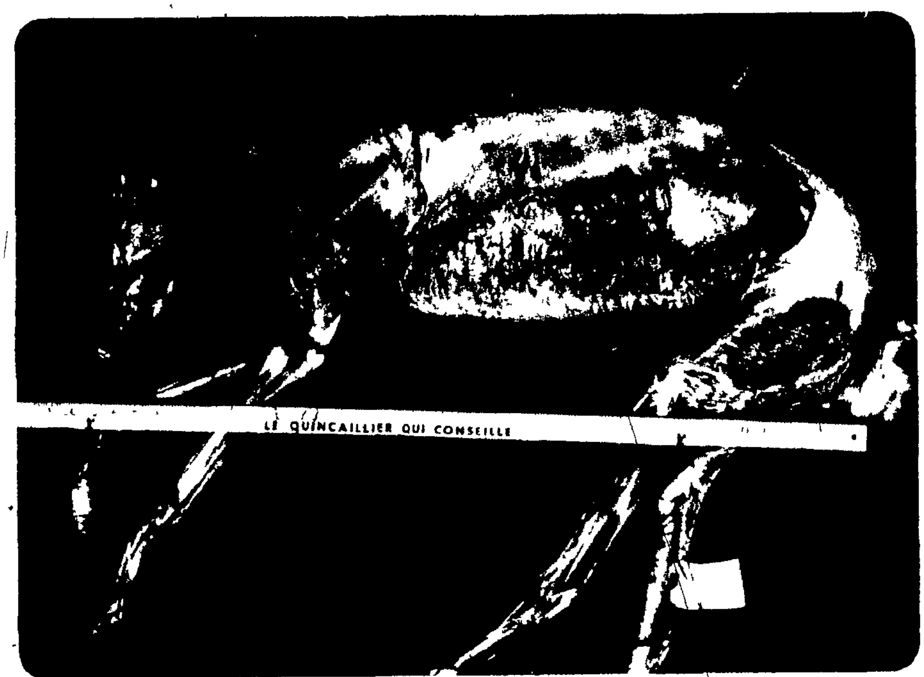
The 13 wolves used in this study were obtained as skinned carcasses (Figure 4-1). Five were juveniles (approximately seven months of age) which had been trapped for their pelts during November, 1981. The other eight wolves (two juveniles and six adults) were shot during February, 1982 as part of an experimental control program. All wolves were collected in, or adjacent to, the northeast section of the La Verendrye Reserve (Figure 4-2). All carcasses had been frozen out of doors before being moved to a freezer at the laboratory. At necropsy, the diaphragm was removed and frozen; later this tissue was digested artificially in a solution of pepsin (0.5 percent) and hydrochloric acid (0.3 percent). The supernatant was decanted and the sediment examined for the presence of <u>Trichinella</u> larvae. Following removal of the viscera, the body cavity was washed with tap water and checked for helminths. The trachea, lungs, heart, oesophagus, stomach, liver, pancreas, spleen and kidneys were examined macroscopically for helminth parasites. Findings were confirmed under a dissecting microscope. The small and large intestines were cut into ten centimeter segments, perfused with water and opened. The intestinal contents, mucosal scrapings and the mucosa itself were examined under magnification (x2). Due to the poor condition of the worms, the intensity of <u>E. granulosus</u> infections could not be accurately ascertained. Infections were therefore classified as being light, moderate or heavy (less then 500, 500 to 5,000, and more than 5,000 worms respectively). Trematodes and cestodes were fixed in alcohol-formalin-acetic acid (AFA) and were identified by comparing those in good condition with known specimens. Nematodes were fixed in a mixture of five percent glycerine and 70 percent alcohol. Faecal samples taken from the rectum were concentrated using the formol-ether technique (Baker, 1969), stained with iodine, and examined for the presence of taeniid eggs.

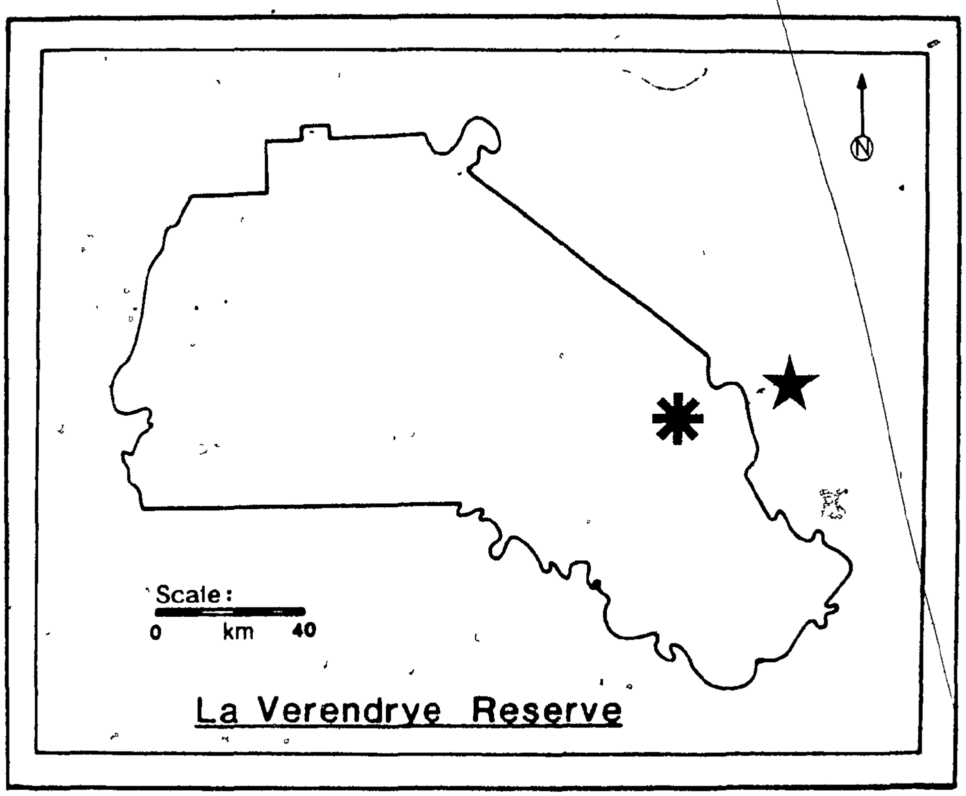
Figure 4-1. Skinned carcass of a wolf from the La Verendrye Reserve.

Figure 4-2. Map of the La Verendrye Reserve indicating areas from which wolves were collected.

✱ Shot wolves

★ Trapped wolves





COLOURED PICTURES
Images en couleur

2. Collection and Examination of Wolf Faeces

Wolf faeces examined during the course of this study had been collected from the ground in the La Verendrye Reserve between July, 1981 and June, 1982. All samples were frozen prior to examination. One to two grams of faeces were taken from the frozen specimens, placed in 10 percent formalin and autoclaved at 120 degrees Celcius for 20 minutes. The samples were then examined as described above and the Chi-square test of independence (Siegel, 1956) was employed to test for significant fluctuations in the prevalence of taeniid eggs.

C. RESULTS

1. Necropsy of Wolf Carcasses

Of the wolves necropsied during this study, eight (62%) were males and five (38%) were females. Young (less than one year) and adult wolves were quite evenly represented in the sample; seven (54%) and six (46%) respectively.

Nine (69%) of the 13 wolves examined harboured helminth parasites. *E. granulosus* was the most prevalent species, occurring in eight (62%) of the wolves. Three other helminth species were found. These parasites, (*Dioctophyma renale*, *Taenia* sp. and *Alaria* sp.) occurred only once (8%) in each of three wolves (Appendix 4-1). Only two wolves harboured concurrent infections (*E. granulosus* with *D. renale*, and *E. granulosus* with *Taenia* sp.). More males (75%) than females (40%) harboured *E. granulosus*.

Equal numbers (four) of young and adult wolves were infected, although the young wolves had predominantly lighter infections (Table 4-2).

Faecal examinations demonstrated the presence of taeniid eggs in only four (50%) of the infected wolves (Table 4-2). It is interesting to note that taeniid eggs were detected in all of the heavy infections whereas only one light infection was positive for egg passage.

2. Coprological Examinations

Results of coprological examinations of wolf faeces collected from the La Verendrye Reserves are shown in Figure 4-3. Prevalence of taeniid eggs in these faecal samples ranged from zero (October, 1981) to 33 percent (January, 1982), with an overall mean of 16 percent. Neither seasonal (November to March, April to October) nor monthly fluctuations in prevalence are statistically significant ($X^2 = 3.84$, df = 1, $p > 0.10$ and $X^2 = 3.12$, df = 1, $p < 0.10$ respectively).

D. DISCUSSION

The prevalence of *E. granulosus* in wolves from the La Verendrye study area is in accordance with values reported by other workers (Table 4-1). Other helminths, however, occurred infrequently in the 13 wolves examined. Although the cysticerci of *Taenia krabbei* and *Taenia hydatigena* have been reported in moose from the La Verendrye Reserve (Ethier, 1976), the occurrence of the adult cestodes in the wolves, as reported herein, is less

Table 4-2. Results of necropsy and coprological examinations of the wolves collected from the La Verendrye Reserve.

WOLF NUMBER	SEX	AGE *	*E. granulosus* PRESENT	INTENSITY OF INFECTION +	TAENIID EGGS PRESENT IN FAECES
1	Male	Young	x	Light	
2	Female	Young			
3	Female	Young			
4	Male	Young	x	Light	
5	Male	Young	x	Light	x
6	Male	Adult			
7	Female	Adult			
8	Male	Adult	x	Heavy	x
9	Male	Young			
10	Female	Adult	x	Light	
11	Male	Young	x	Heavy	x
12	Female	Adult	x	Heavy	x
13	Male	Adult	x	Moderate	

* Young = less than one year

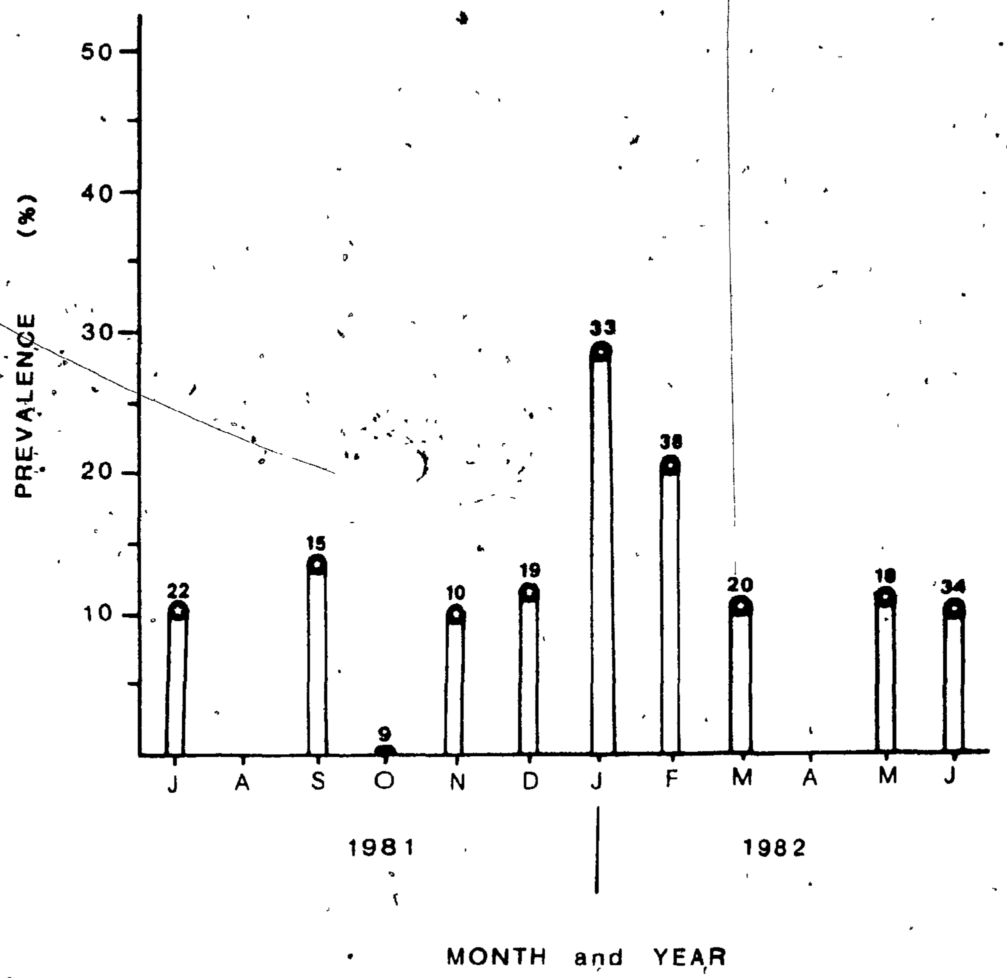
Adult = more than one year

+ Light = less than 500 worms

Moderate = 500 to 5,000 worms

Heavy = more than 5,000 worms

Figure 4-3. Monthly prevalence (%) of taeniid eggs in wolf faeces from the La Verendrye Reserve (1981/1982). Numbers above bars represent sample sizes.


PREVALENCE (%)
50
40
30
20
10
22
15
9
10
19
33
38
20
18
34
J
A
S
O
N
D
J
F
M
A
M
J
1981
1982
MONTH and YEAR

frequent than that reported in previous studies (Freeman _et al._, 1961; Holmes and Podesta, 1968; Trudeau, 1981). Freeman (1961) stated that _E. granulosus_ may be twice as prevalent in wolves as are _T. krabbei_ or _T. hydatigena_ in areas where moose are more numerous than deer. Because the La Verendrye Reserve is situated at the northern limits of the deer range, moose are virtually the only ungulate inhabiting this area (Messier, 1980). As such, moose do predominate in the diet of wolves from this area (60 percent of the summer diet and 90 percent of the winter diet) (Messier, 1981). This may, in part, account for the apparent dearth of other taennid species in the wolves sampled. The precise causes, however, remain obscure. The wolves necropsied during the present study were collected in the winter months, as were most of the wolves examined in previous studies (Freeman et al., 1961; Holmes and Podesta, 1968; Choquette et al., 1973; Samuel et al., 1978). Thus, helminths which occur in wolves other than during the winter would not be found in wolves sampled during this season. Ideally, wolves should be sampled throughout the year before a realistic estimate of parasite burden may be obtained.

The prevalence of taeniid eggs in both rectal and field-collected faecal samples indicates that coprological examinations do not yield an accurate estimate of _E. granulosus_ infections in a free-ranging wolf population. All of the heavily parasitized wolves (as demonstrated by necropsy) gave positive coprological results, whereas only one lightly infected individual did so. In addition, the presence of taeniid eggs in faeces collected from the La Verendrye Reserve during the same period as the 13 wolves, indicated a prevalence of 20 percent. That wolves from this area showed an actual prevalence of 62 percent suggests that two-thirds of _E. granulosus_ infections in these hosts may escape detection by coprological examination.

Wolves are generally considered to be relatively inefficient predators and extensive travel within a pack's territory (up to 107 kilometers) is often necessary to locate vulnerable prey (Mech, 1970; Allen, 1979). Thus, it may be that the relatively high prevalence of _E. granulosus_ infections in wolves, reported in this and previous studies (Table 4-1), is required to distribute the infective stages throughout the environment, thereby generating the observed levels of parasitism in the coexisting moose population.

CHAPTER V. OVERVIEW

A composite of this and previous studies points to a geographic homogeneity, particularly in the intermediate host, of Echinococcus granulosus infection levels wherever moose and wolves coexist in North America. The present study suggests that sylvatic echinococcosis is a stable endemic infection of moose and wolves in southwestern Quebec. Data presented in the preceeding chapters may be examined in the light of what is known about factors which may influence the stability of host-parasite relationships.

Wolf packs occupy large territories, the boundaries of which change with time due to changing patterns of prey density and pack composition (Mech, 1970; Allen, 1979; F. Messier, unpublished data). Such movements of infected wolves would contribute to the contamination of the study areas. Since E. granulosus eggs are very resistant to environmental extremes (Sweatman and Williams, 1963b), this dissemination of infective stages by the wolves may represent a continuing source of infection for the moose population occupying these areas. The predominance of moose in the diet of these wolves, in conjunction with the prevalence of infection (44 percent) in the moose population and the high proportion (86 percent) of viable protoscoleces, ensures the successful completion of this parasite's life cycle.

Anderson (1978) discusses a number of population processes which may influence the stability of natural host-parasite associations. Some of these processes may well be acting upon the sylvatic cycle of E. granulosus in the study areas. The presence of regulatory factors such as overdispersion, and the absence of destabilizing factors such as parasite-induced reduction of host reproduction potential or direct parasite reproduction within the host (Anderson, 1978), might contribute to the apparent stability of E. granulosus infection levels in southwestern Quebec. The significance of parasite-induced susceptibility to predation in this host-parasite relationship may be in facilitating transmission. Holmes and Bethel (1972) stated that "where the predator is an inefficient one, the strategy of the parasite could include decreasing the stamina of the prey, making it more conspicuous, or affecting its ability to respond to the predator". Given that wolves are inefficient predators (Mech, 1970) and given the pattern of E. granulosus in the moose population, parasite-induced susceptibility to predation may be of adaptive significance to this parasite.

When assessing the significance of E. granulosus infections in the moose population, it must be remembered that several factors, mainly predation and food supply, interact to regulate moose numbers. It is not likely that parasitism by E. granulosus exerts a major influence on the population dynamics of this intermediate host species. Nevertheless, it may play a modulating role in the predator-prey relationship between moose and wolves and therefore must be considered when studying the ecology of these two host species. Indeed, helminths in general, and particularly their larval stages, may be important factors in the population dynamics and ecological relationships of wild animals. An awareness of the complex relationships between parasites and their hosts, and the possible significance of such infections, is crucial to an improved understanding of the ecology of wildlife communities.

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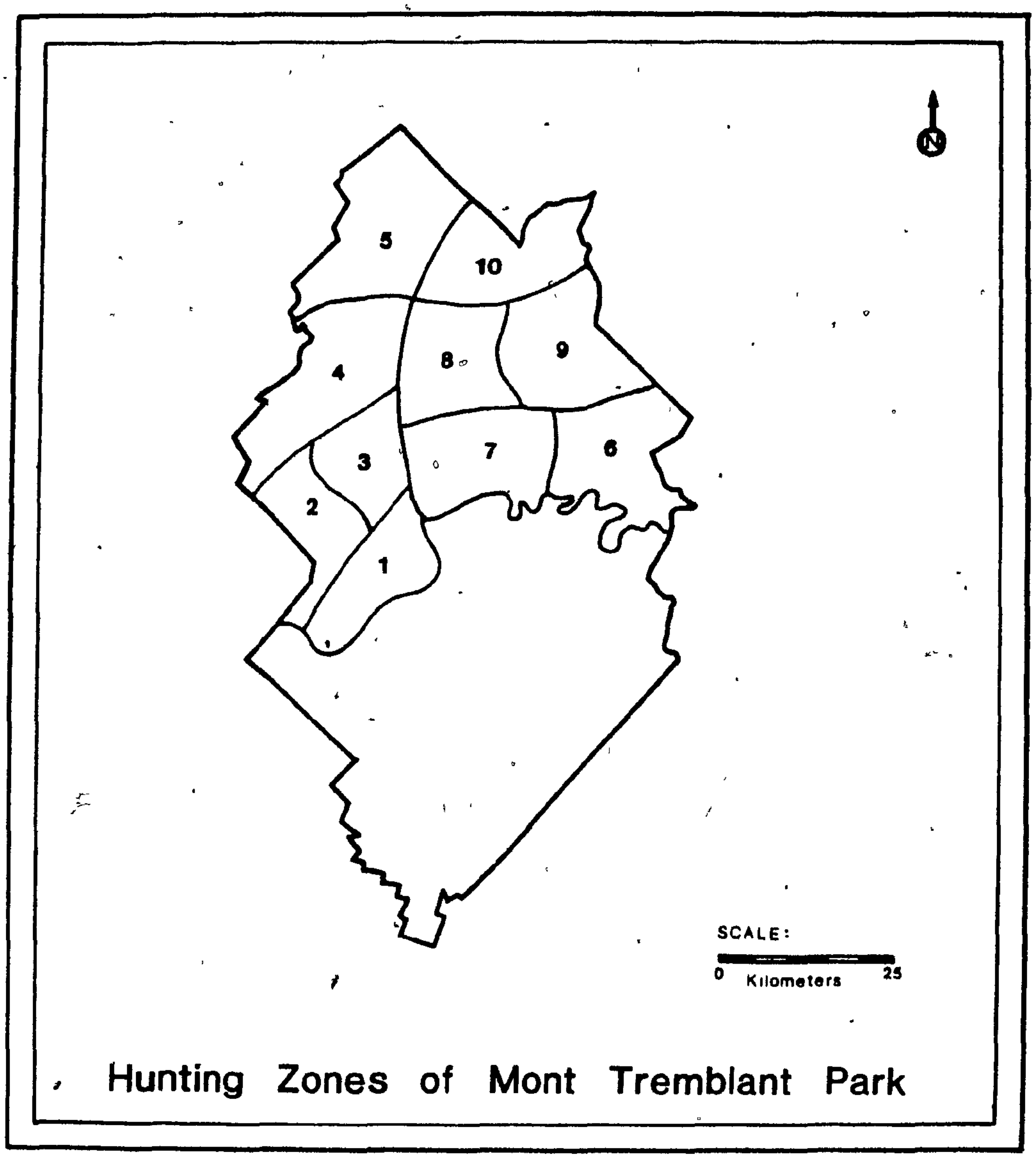
Appendix 3-1. Duration of annual moose hunts in the three study areas (1978 - 1981).

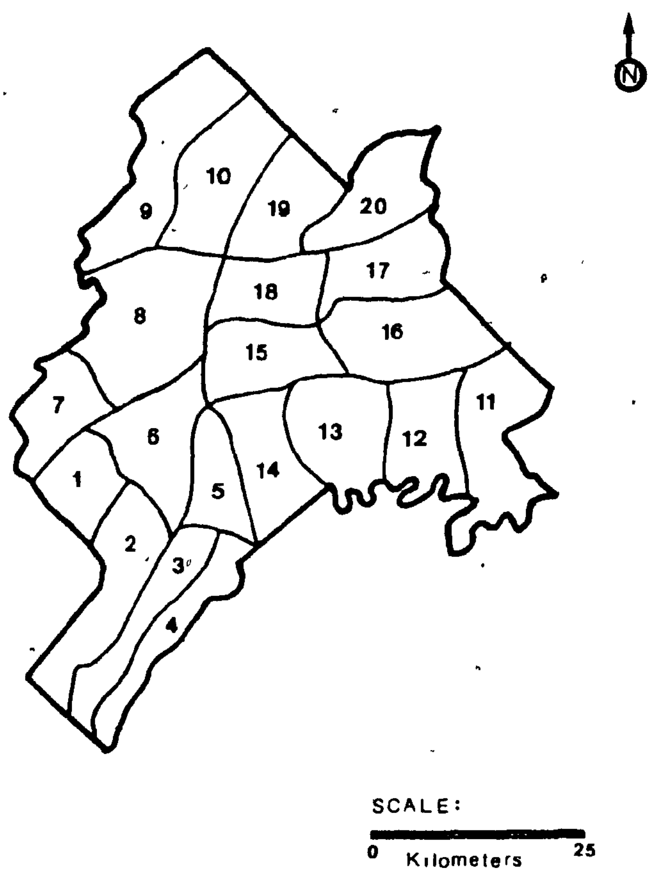
YEAR	RESERVE					
	Rouge-Matawin		La Verendrye		Mastigouche	
	Hunting Period	No. of Days	Hunting Period	No. of Days	Hunting Period	No. of Days
1978	22 Sept to 23 Oct	32				
1979	17 Sept to 26 Oct	40				
1980	22 Sept to 24 Oct	33	20 Sept to 19 Oct	29		
1981	18 Sept to 3 Oct	16*	19 Sept to 18 Oct	29	3 Oct to 23 Oct	20

* The shorter hunt in 1981 is due to an increase in the number of hunting zones of this reserve (page 15).

Appendix 3-2. Hunting zones of Mont-Tremblant Park.

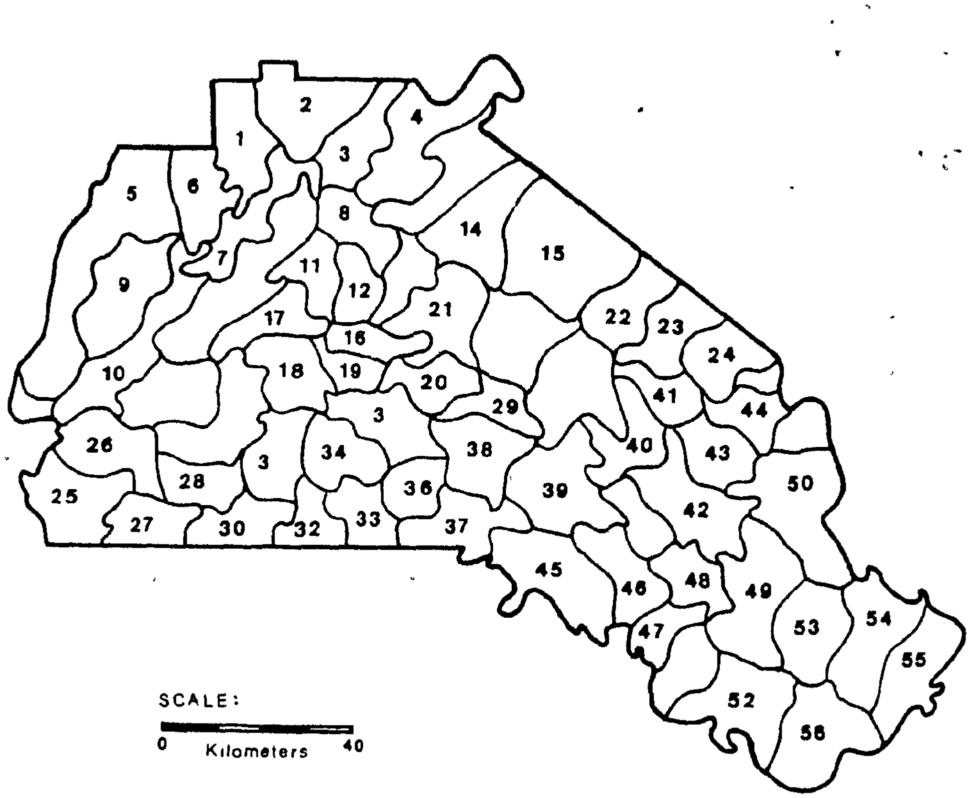


Appendix 3-3. Hunting zones of the Rouge-Matawin Reserve.



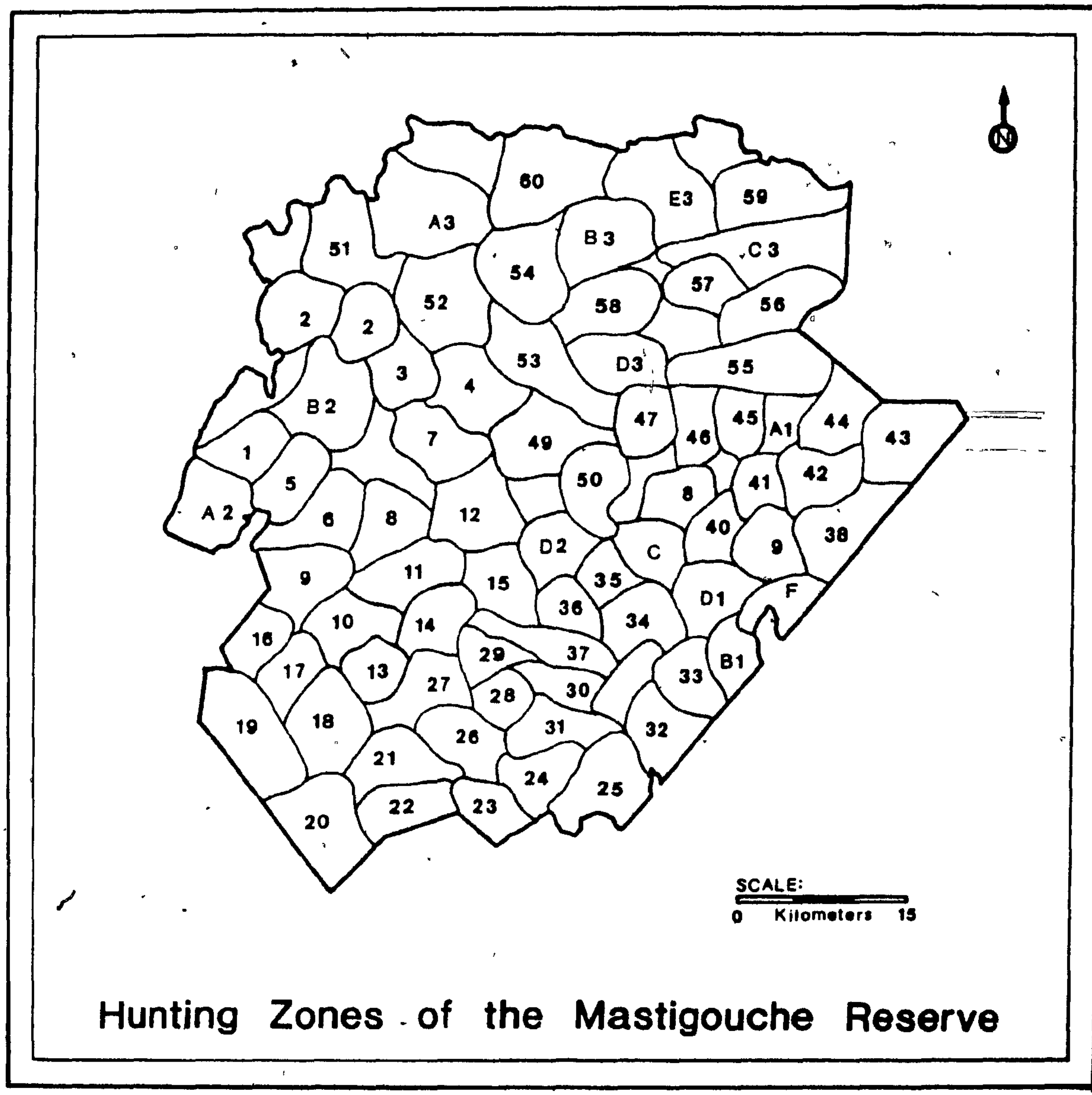
Hunting Zones of
the Rouge-Matawin Reserve

Appendix 3-4. Hunting zones of the La Verendrye Reserve.



Hunting Zones of the La Verendrye Reserve

Appendix 3-5. Hunting zones of the Mastigouche Reserve.



Appendix 3-6. Letter requesting hunters to collect moose lungs.

A TOUS LES CHASSEURS:

L'Institut de Parasitologie de l'Université McGill, avec l'aide du Ministère du Loisir, de la Chasse et de la Pêche, conduit une étude sur les parasites de l'orignal. Un de ces parasites, une larve de ver plat, se retrouve au niveau des poumons de l'orignal et porte le nom de "kyste hydatid". Lorsque les loups ingèrent les orignaux infectés, la larve se transforme en adulte dans l'intestin du loup. Le cycle de vie de ce parasite est schématisé au verso de cette feuille.

Ces derniers années, les chasseurs de la Réserve de La Vérendrye et de la Reserve Rouge-Matawin (autrefois appele Parc Mont-Tremblant) ont aidé a cette étude en apportant les poumons des orignaux lorsqu'ils venaient enregistrer leur prise. Nous vous demandons de nous aider à poursuivre cette étude en déposant les poumons <u>entier</u>, avec la trachée si possible, dans un sac en plastique qui vous sera fourni. Veuillez retourné celui-ci au biologiste du parc lors de l'enregistrement de votre orignal.

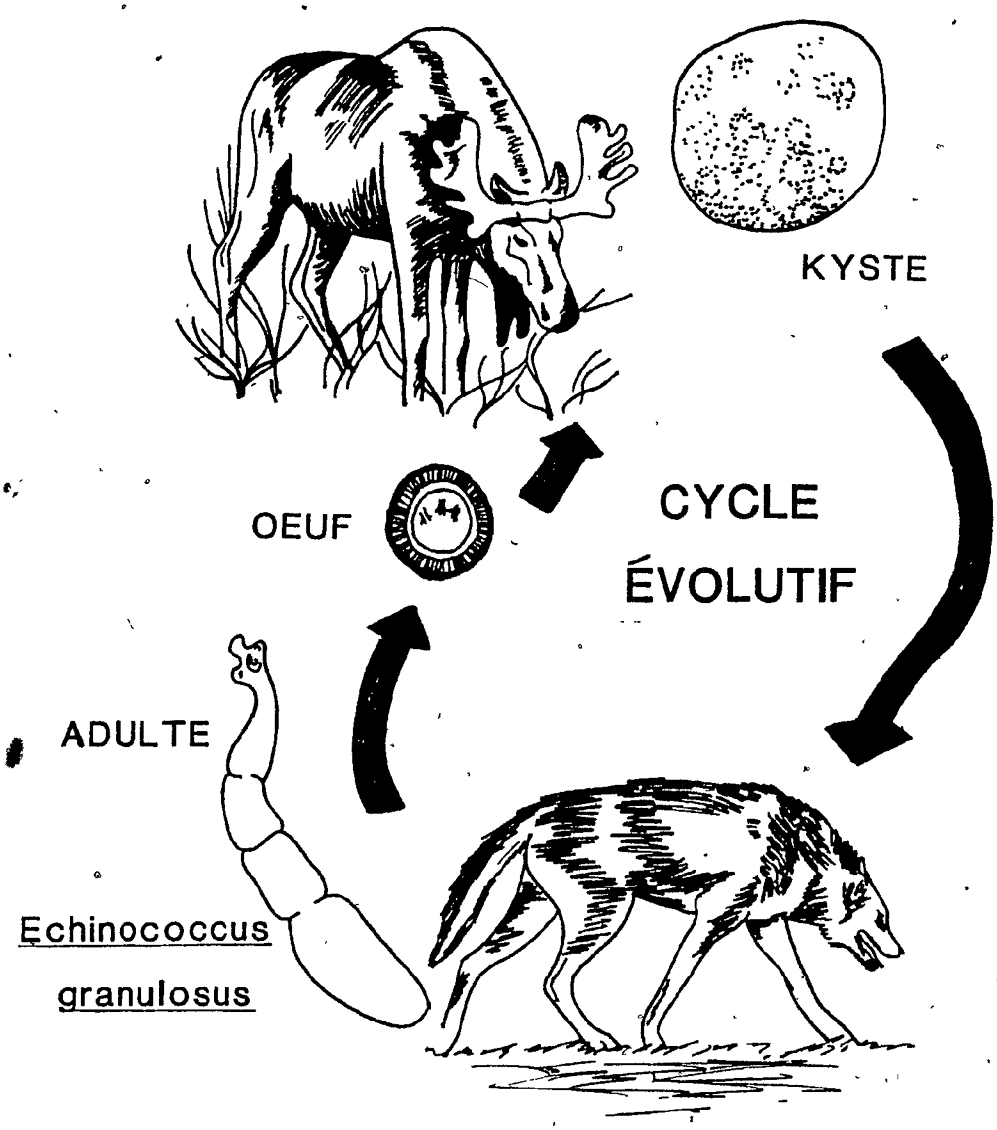
Il est important de ne pas laisser les poumons dans les bois car les loups peuvent les ingérer et ainsi augmenter le risque d'infections chez l'orignal. Les larves dans les poumons ne sont pas directement transmissibles à l'homme. Toutefois, il faut éviter de donner des poumons infectés aux chiens car les vers adultes se développent dans leurs systèmes; par la suite, les oeufs de parasites contenus dans les excréments des chiens peuvent contaminer l'homme, ce qui peut être très dangereux.

Nous vous remercions de votre collaboration et vous souhaitons une bonne chasse!

Marilyn A. McNeill — Manfred E. Rau

L'Institut de Parasitologie, L'Université McGill

Appendix 3-7. Diagram of the life cycle of Echinococcus granulosus distributed to hunters during pre-hunt interviews.



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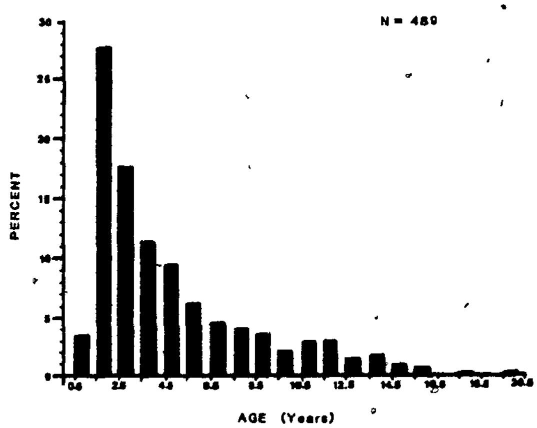
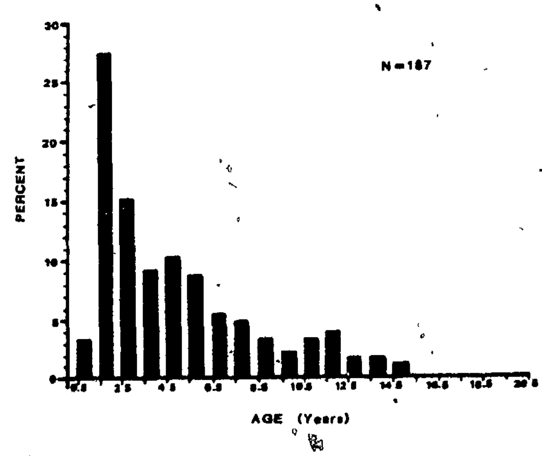
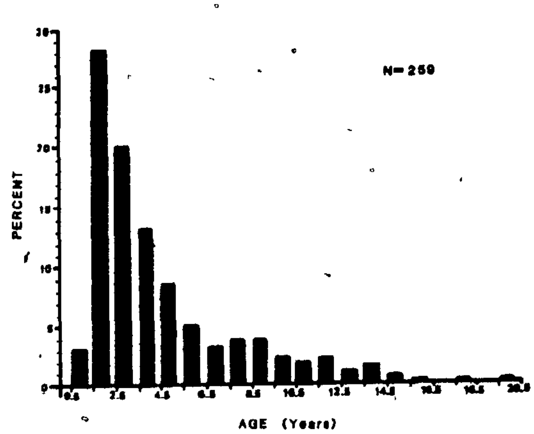
Appendix 3-8. Age distribution of moose shot during the annual hunts.



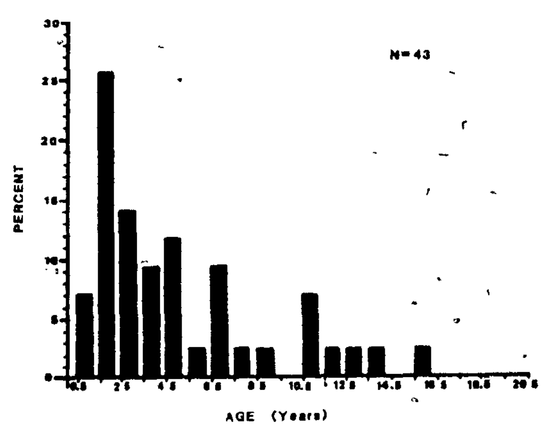
Overall



Rouge-Mätawin (1978 to 1981)



La Verendrye (1980, 1981)



Mastigouche (1981)

Appendix 3-9. - Abundance, mean intensity, mean cyst weight, and biomass of infection for moose shot during the annual hunts in the three study areas.

PARAMETER	SAMPLE							TOTAL
	Rouge-Matawin				La Verendrye		Mastigouche	
	1978	1979	1980	1981	1980	1981	1981	
Abundance	14.4 (3.84) n=45	7.3 (2.98) n=54	9.6 (2.56) n=46	9.1 (3.83) n=42	8.6 (1.46) n=137	10.0 (2.60) n=122	5.5 (1.82) n=43	9.2 (1.01) n=489
Mean Intensity	25.0 (5.86) n=26	20.8 (7.67) n=19	15.2 (3.70) n=29	21.2 (8.23) n=18	18.2 (2.61) n=65	28.9 (6.82) n=42	15.6 (4.13) n=15	21.0 (2.05) n=214
Mean Cyst Wt. (grams)	*	*	2.7 (0.35) n=29	1.9 (0.19) n=18	2.2 (0.22) n=65	2.5 (0.25) n=42	2.1 (0.87) n=15	2.2 (0.12) n=169
Biomass (grams)	*	*	43.6 (9.41) n=29	59.2 (28.11) n=18	53.3 (10.64) n=65	104.8 (29.29) n=42	41.2 (14.24) n=15	63.9 (86.96) n=169

( ) Figures in brackets represent one standard error.

* Cyst weight was not available for 1978 or 1979 data.

Appendix 4-1. Helminths of wolves from the La Verendrye study area.

HELMINTHS	SITE	PREVALENCE (%)	Number examined
Trematode			
Alaria sp.	si *	8	(1/13)
Cestodes			
Taenia sp.	si	8	(1/13)
Echinococcus granulosus	si	62	(8/13)
Nematode			
Dioctophyma renale	kidney	8	(1/13)

* si = small intestine