THE HELMINTHOFAUNA OF SMALL RODENTS IN SOUTHERN MANITOBA

A Thesis

Presented to

the Faculty of Graduate Studies and Research

University of Manitoba

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Brian Richard Jacobsen

ABSTRACT

Eleven species of helminths (seven of cestodes and four of nematodes) were found in a total of 1081 specimens of five species of rodents from southern Manitoba. Six new host records were established. Focal distributions of cestodes were attributed to their life cycles; and foci of nematodes to the relative abundance of moisture in the habitats studied. Infections of Andrya macrocephala and Capillaria hepatica varied seasonally. No statistical evidence was found of positive or negative correlative occurrence between members of parasite pairs. Capillaria hepatica was the only rodent parasite found that is a potential human pathogen. Cuterebra sp. (Cuterebridae: Diptera) was found in 5.5% of rodents examined.

ACKNOWLEDGMENTS

I would like to express my sincere gratitude to Dr. G. Lubinsky, Associate Professor of Zoology, University of Manitoba for his assistance and encouragement in this study. I am also indebted to Dr. H. E. Welch, Head, Department of Zoology, University of Manitoba, for his valuable counsel. Thanks are due to Dr. C. Watts, Department of Zoology, University of Manitoba, Dr. S. Iverson of the Whiteshell Nuclear Reactor at Pinawa, Manitoba and Dr. M. Levin of the Department of Botany, University of Manitoba.

TABLE OF CONTENTS

Table of Contents (continued)

LIST OF TABLES

LIST OF FIGURES

List of Figures (continued)

INTRODUCTION

The helminthofauna of small rodents has been well studied in the northern United States and in eastern and western Canada, but little is known of rodent helminths in Manitoba and Saskatchewan. The purpose of this work was, therefore, to extend the knowledge of the distribution of these helminths in Manitoba.

The results of this type of survey are better understood if the habitat and habits of the host are considered, as the external environment often influences the host and hence its parasite fauna. This influence of habitat is reflected not only in the number and variety of helminths infecting the rodents, but also in the seasonal changes of the parasite fauna.

Three other aspects of parasitism were also examined: multiple species parasitism, focal distributions of helminths, and the existence in Manitoba of rodent parasites which are potential human pathogens.

To obtain the required data, rodents were trapped in five different biotopes in southern Manitoba during May to September in 1966 and 1967.

HISTORICAL REVIEW

The helminthofauna of small rodents has been intensively studied in the northern United States, but only a few papers on the helminths of Canadian rodents have been published (Table I). Previous Canadian workers (35,46,53,70,90) were concerned with either a specific rodent or a helminth (e.g.larval cestodes). Schad (89) and Lubinsky (65) studied the parasites of several rodents, but gave no data about differences between biotopes, seasonal variation, or multiple species parasitism.

In the United States, Harkema (45) studied seasonal variation in helminth infections of the rabbit, but not of the rodents that he examined. Rausch and Tiner (85) also studied seasonal variation, but did not analyse the differences between helminth infections in the various biotopes which they examined. Kuns and Rausch (56) are the only known workers who analysed the differences between biotopes and their influence on the parasites of voles from these biotopes. The remaining American workers have provided only lists of the rodents that they examined and the parasites that they found.

My study, therefore, represents probably the only study of this type in North America, as it examines several aspects of parasitism.

TABLE I.

Previous surveys of the helminthofauna of small rodents in Canada and in the north central United States.

DATE		
CANADA		
1933	McLeod (70)	Manitoba*
1951	Knight (53)	British Columbia
1954	Schad (89)	N.E.Quebec & Labrador
1956	Schad (90)	S. Quebec
1957	Lubinsky (65)	Alberta
1959	Freeman and Wright (35)	Ontario
1966	Hnatiuk (46)	Saskatchewan
UNITED STATES		
1915	Barker (7)	United States
1936	Harkema (45)	North Carolina
1938	Erickson (29)	Minnesota
1942	Ameel (3)	Michigan
1948	Rausch and Tiner (85)	North-central States
1949	Edwards (26)	New York
1950	Kuns and Rausch (56)	Wyoming
1952	Rausch (80)	Alaska
1957	Dunagan (24)	Alaska
1953	Read and Millemann (86)	California
1953	Sillman (94)	Michigan
1955	Hall and Sonnenberg (43)	Maryland, Kentucky
1960	Grundmann (39)	Utah
1962	Leiby (58)	Idaho
1967	Kinsella (51)	Montana

*McLeod studied only the genus Citellus in Manitoba.

DESCRIPTION OF THE SURVEY AREAS

Five different biotopes were selected for this survey in order to determine how the parasitic fauna of rodents varies with the habitat of the host. These biotopes were disturbed grassland, lakeshore forest, backshore marsh, open fields, and aspen-ash forest.

The climate of the first three biotopes is nearly identical: the mean July temperature is 68-69° F. and the mean January temperature 1-2° F. The frost-free season lasts 110-120 days. Average annual precipitation is 19-20 inches. The climate of the open fields and aspen-ash forest is cooler and wetter: the mean July temperature is 66-67° F. and that of January-1-0° F. The frost-free season lasts 100-110 days. Annual precipitation is 21-22 inches. These data are taken from meteorological records of the Meteorological Division, Department of Transport and are from recording sites as close as possible to the collection or study sites.

The following descriptions of the trapping areas include the soil, flora, and rodents. The rodents recovered from each area are listed in Table II. Botanical nomenclature is that used by Scoggan (92).

AREA I - DISTURBED GRASSLAND

Fields of this type were examined at Emerson, Treherne, and Winnipeg (Fig.1):

(a) Soil: black and fine-textured, overlaying a grey,

TABLE II.

Rodents recovered from each of the five biotopes.

	AREA I	AREA II	AREA III	AREA IV	AREA V	TOTAL
Microtus pennsylvanicus drummondi	465	14	125	117	3	724
Clethrionomys g. gapperi				2	56	58
C. gapperi loringi	2	216	2			220
Peromyscus m. maniculatus					18	18
P. maniculatus bairdi	6	24				30
Zapus h. hudsonius				3	1	4
Zapus hudsonius campestris		4	2			6
Napeozapus insignis frutectanus					1	1
TOTALS	473	258	129	122	79	1061

Figure 1. Map of southern Manitoba showing the trapping areas.

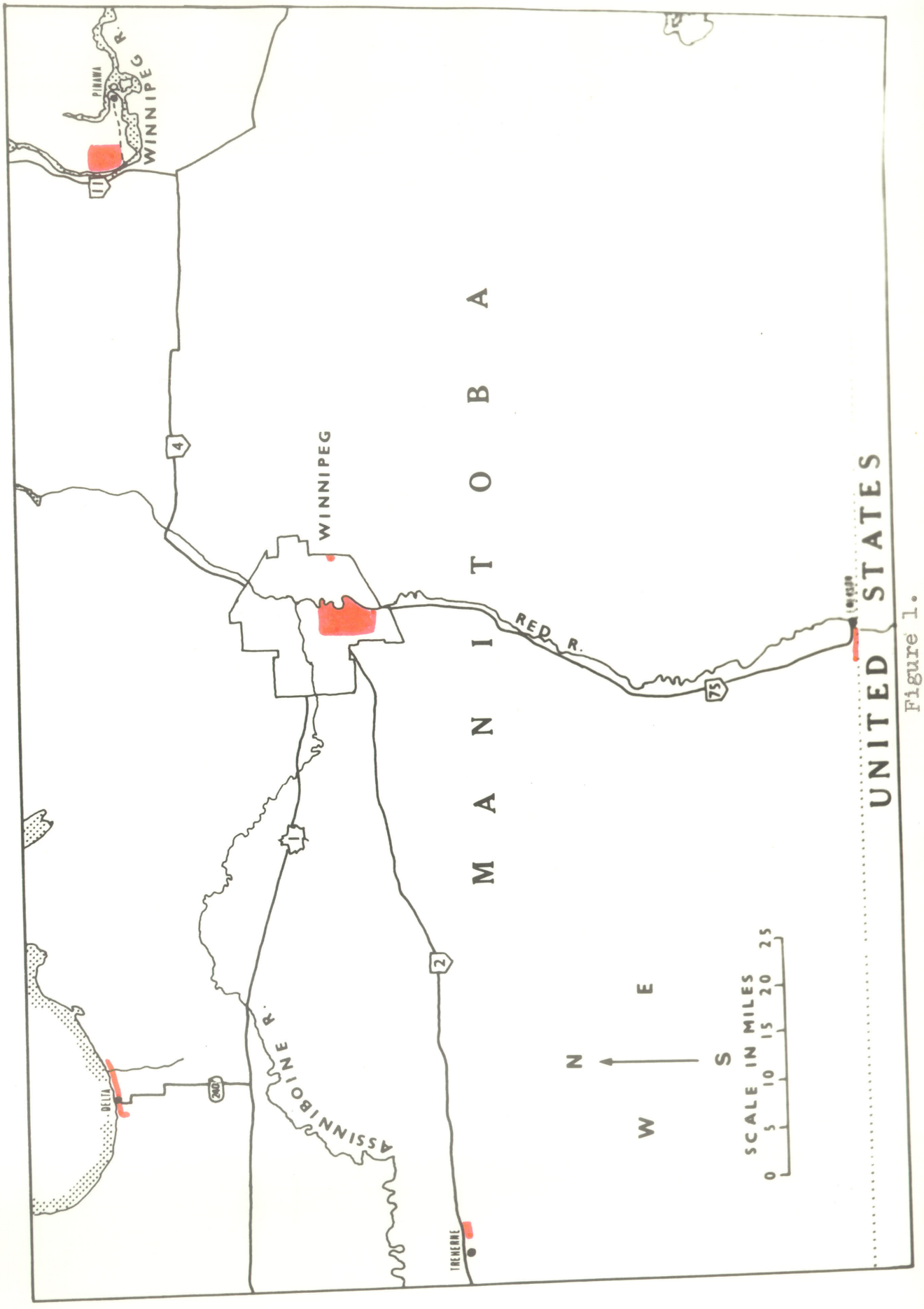
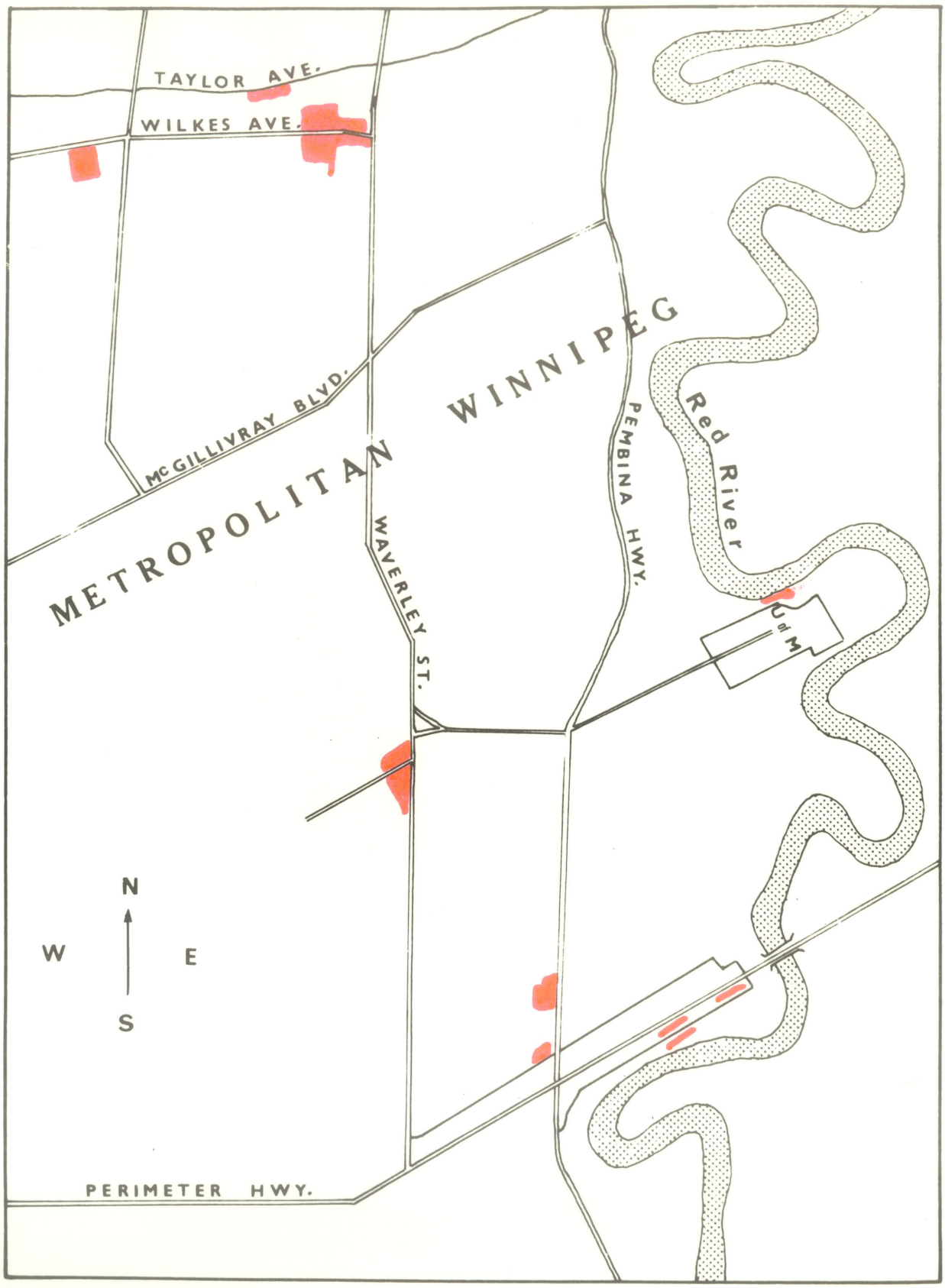

PINAWA R.
WINNIPEG
11
4
WINNIPEG
MANITOBA
RED R.
73
UNITED STATES
1
2
ASSINIBOINE R.
DELTA
2NO7
IRENEMNE
N
W
E
S
SCALE IN MILES
0 5 10 15 20 25

Figure 1.

Figure 2. Map of south Winnipeg showing the trapping areas of the disturbed grassland biotope.



SCALE 1: 48,300

Figure 2.

moist clay. Drainage was good due to the abundance of adjoining ditches.

(b) Flora: grass (Agropyron repans) and field melilot (Melilotus alba) formed a thick mat on the fields. Goldenrod (Solidago sp.) and aster (Aster ericoides) were common. Cockleburr (Xanthium italicum) and Rumex crispus were scattered throughout the fields. Rhus typhina, wild rose (Rosa arkansana), and snowberry (Symphoricarpos sp.) were found in localized clumps.

(c) Rodents: the main rodent trapped here was Microtus pennsylvanicus drummondi (Audubon and Bachman). A few specimens of Clethrionomys gapperi loringi (Bailey) and Peromyscus maniculatus bairdi (Hay and Kennicott) were also recovered.

AREA II - LAKESHORE FOREST

This biotope was characterized by a sand ridge that runs along the southern edge of Lake Manitoba at Delta. It is essentially a flood plain that is flooded every ten years (62) (Fig.3). Walker (106) described the flora of the Delta Marsh in 1959, this was later revised by Levin (62) in 1968.

(a) Soil: sandy loam on gravel and coarse sandy beach deposits. Drainage is good on the crest of the ridge and poor at the edges.

(b) Flora: the ridge is heavily wooded with green ash (Fraxinus pennsylvanica) and Manitoba maple (Acer

Figure 3. Map of Delta region showing the positions of biotopes II and III.

II

III

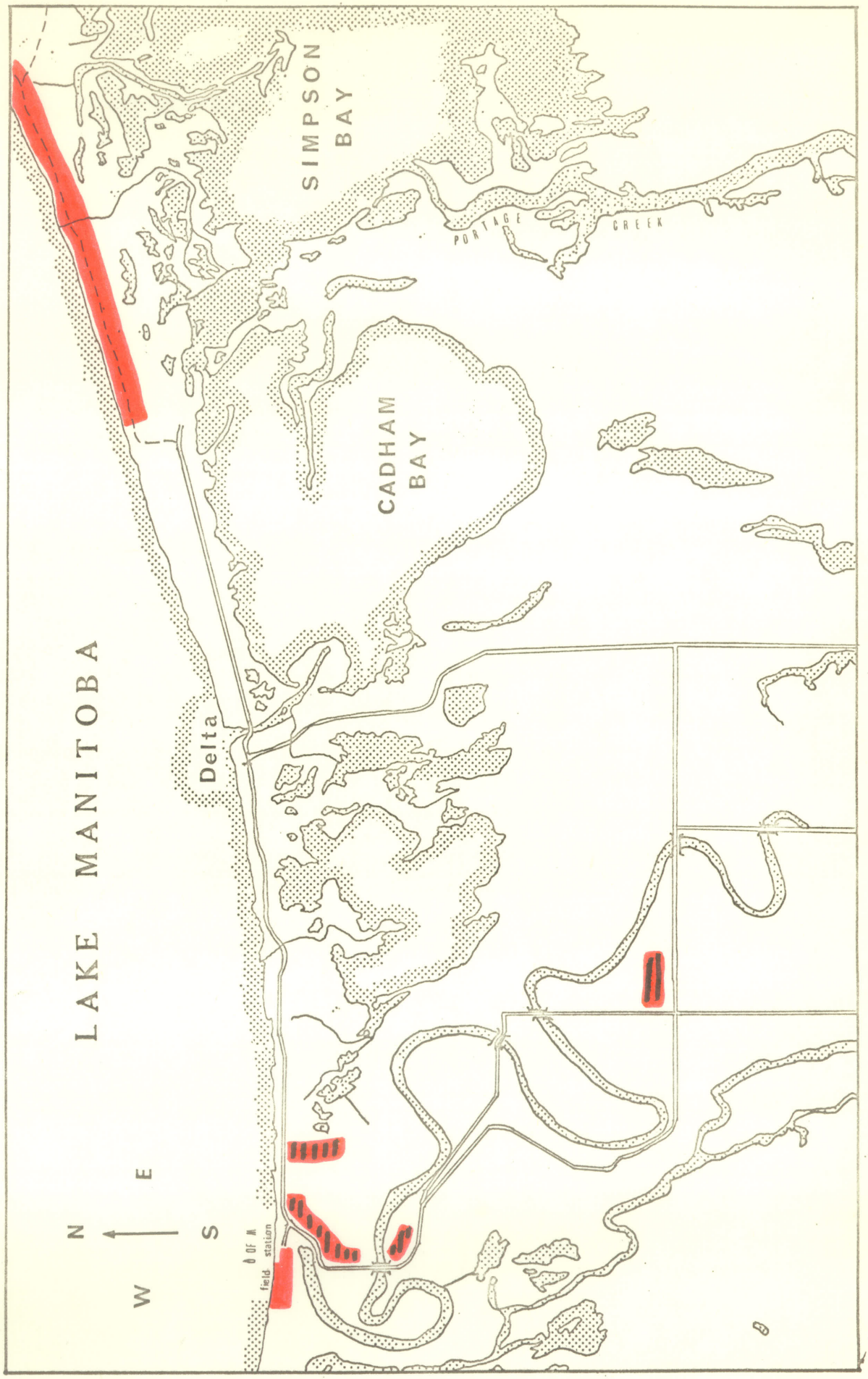

LAKE MANITOBA
SIMPSON BAY
PORTAGE CREEK
CADHAM BAY
Delta
field station
N
S
E
W
SCALE 1:50,000
1 Mile

Figure 3.

negundo); cottonwood (Populus deltoides) was scattered along the ridge. Shrubs were represented by 7 species of willows (Salix spp.), choke cherry (Prunus virginiana), and blackberry (Rubus pubescens). Couch grass (Agropyron repans) and stinging nettle (Urtica dioica) were the dominant herbs (62).

(c) Rodents: large populations of C. g. loringi and P. m. bairdi were found in the forest. Small numbers of M. p. drummondi were found in grassy areas of the forest.

AREA III - BACKSHORE MARSH

A portion of the Delta marsh near the University of Manitoba Field Station comprised Area III. This was a backshore marsh separated from Lake Manitoba by the sand ridge and lakeshore forest.

(a) Soil: thin muck and peat deposits overlaying variable glacial drift deposits. The depth of peat covering the mineral soil is variable, but is usually relatively thin. Some portions become dry as summer progresses.

(b) Flora: the dominant plant species here is whitetop (Scholochloa festucacea) with late dominance by Sonchus arvensis. Phragmites communis was scattered throughout this portion of the marsh.

(c) Rodents:dense populations of M. p. drummondi were found in 1966 along with a few C. g. loringi and

Zapus hudsonius campestris (Preble). Trapping failed to yield any rodents in 1967.

AREA IV - OPEN FIELDS

These are similar to those of Area I, but rural and situated in the mixed transition zone of eastern Manitoba at the Whiteshell Nuclear Reactor Establishment at Pinawa (Fig.1).

(a) Soil: the topsoil is dark and covers a layer of clay. Drainage varies from poor to good.

(b) Flora: the grass cover (Agropyron sp.) was tall and thick. Sedge (Carex spp.) occurred in wetter areas. Willow (Salix spp.) was found in the wetter fields and aspen (Populus tremuloides) in the drier.

(c) Rodents: large populations of M. p. drummondi were found. A few Clethrionomys gapperi gapperi (Vigors) and Zapus hudsonius hudsonius (Zimmermann) were also trapped.

AREA V - ASPEN-ASH FOREST

This was situated at Pinawa along the eastern bank of the Whiteshell River.

(a) Soil: same as that of Area IV. Drainage is good.

(b) Flora: heavily wooded with aspen poplar (Populus tremuloides) and ash (Fraxinus sp.). White birch (Betula papyrifera) and bur oak (Quercus macrocarpus) were also present. Herbs were represented

by poison ivy (*Rhus radicans*), swamp raspberry (*Rubus pubescens*), and wild strawberry (*Fragaria virginiana*).

(c) Rodents: large numbers of *C. g. gapperi* and *Peromyscus maniculatus maniculatus* (Wagner) were found with a few *M. p. drummondi*. One specimen each of *Z. h. hudsonius* and *Napeozapus insignis frutectanus* (Jackson) were caught.

MATERIALS AND METHODS

COLLECTION OF RODENTS

In addition to personal trapping in Areas I, II, and III, rodents were obtained from Dr. C. Watts of the University of Manitoba Field Station at Delta, from Area III, and from Dr. S. Iverson of the Whiteshell Nuclear Reactor at Pinawa from Areas IV and V. In each instance the methods of trapping and preservation of material were different, and these will be described separately:

Personal trapping: Three types of traps were used:

(a) Victor M-1 snap traps with metal triggers baited with a mixture of peanut butter and oatmeal (12), or plain oatmeal. Both baits gave satisfactory results, though plain oatmeal was easier to store and handle.

(b) Sherman live traps baited with the above baits. These were metal box traps with spring doors: length 9", width 3", height 3". These traps could be used only in spots shaded from the sun as they became hot in direct sunlight.

(c) Metal cylinders 12" long, 6" in diameter, open at one end and inserted into the ground flush with surface and baited with peanut butter and oatmeal. This trap was patterned after one developed by Buchner, 1955 (11).

Snap traps were used the most often. Death was due usually to breakage of the neck or spinal column. No

damage to viscera occurred except in a few cases,and even then the parasites were not harmed.

A disadvantage of the snap trap was that captured rodents could be carried off or eaten by predators. This occurred only in a small percentage of cases: the head was the only portion of the body left in the trap; the digestive tract was lost. Care was taken to conceal the traps so that they were not carried off by birds of prey and crows as happened in one field in southwestern Winnipeg.

The traps were placed so as to obtain the largest number of rodents: saturation trapping. The traps were placed either in long rows along ditches, or in checkerboard fashion at intervals of 5 to 7 yards in fields. Traps were placed in nearby runways or suitable looking spots. The ends of each row were marked with 3/8 inch diameter dowels 48 inches long with strips of coloured cloth attached to the top. The traps were inspected in early morning and in evening, the rodents removed and placed in plastic bags, and the traps rebaited. Each field was trapped for one week at a time.

The rodents were brought to the laboratory and sprayed with the insecticide "Raid" to kill any ectoparasites. If the rodents could not be dissected immediately, they were placed in a 0° F. freezer in order to freeze them as quickly as possible.

Material from Dr. C. Watts: These rodents were trapped mainly with Sherman live traps, placed in pairs at intervals

of thirty metres for population studies; snap traps were also used occasionally. Animals captured alive were killed by a sharp blow to the head, and either frozen or preserved in 15% formalin. Animals preserved in formalin were more difficult to examine for helminths as the internal organs became rigid. Frozen animals were satisfactory for helminthological investigation though histological examination showed that the cells were damaged.

Material from Dr. S. Iverson: Museum special snap traps baited with a mixture of peanut butter, oatmeal and bacon were used. Trap lines were set out according to the method of the International Small Mammal Census. The animals were skinned first, tagged, and then frozen.

Helminths were not damaged in all three methods of trapping.

IDENTIFICATION OF RODENTS

Rodents were identified by each collector. Those collected by myself were identified by using both Peterson (75) and the Criddle collection of the University of Manitoba Zoology Department. Rodents from Pinawa were identified by Dr. S. Iverson using Gunderson and Beer (40), Peterson (75), and Bailey (6). Dr. Watt's sources are unknown.

EXAMINATION OF HOSTS

After the rodents were sprayed to kill ectoparasites,

or after frozen specimens had thawed, they were placed ventral side up on a dissecting board, and a mid-ventral incision made from the urinary papilla to the throat, and skin reflected to each side.

A piece of abdominal musculature was first removed and examined for Trichinella by means of a compressorium and a dissecting microscope. The subcutaneous tissue was then examined for larval helminths, as were the lungs, liver, spleen, mesenteries and kidneys.

The digestive tract was removed and placed in a 2.5% aqueous solution of $MgCl_2$. The tract was slit lengthwise with fine scissors and examined for helminths. The intestinal contents were examined with a dissecting microscope on a black background. Helminths were placed into fresh $MgCl_2$ solution and allowed to relax and die. Cestodes, after death, were compressed slightly between two microscope slides and fixed in F.A.A. (40% formaldehyde 15 c.c., 95% ethanol 85 c.c., glacial acetic acid 5 c.c.). Encysted cestodes and nematodes were fixed in F.A.A. or 10% formalin.

PREPARATION OF CESTODES

The adult cestodes were:

1) washed in water to remove fixative,

2) transferred to a Petri dish with Ehrlich's haematoxylin which had only half the normal amount of stain,

3) stained for twenty-four hours,

4) destained in acid alcohol,

5) blued in running tap water,

6) dehydrated in an ascending series of alcohol,

7) cleared in xylene, and

8) mounted in Permount.

A number of different mounting media were tried: DPX, Histoclad, Crystalite, and Permount. The last gave the least shrinkage upon drying.

Encysted cestode larvae were removed from the cyst and cleared in 85% lactic acid U.S.P. for twelve to twenty-four hours; the acid also dissolved the calcareous corpuscles. The larvae then were placed on a slide in a drop of lactic acid and flattened by gently pressing the conerslip.

PREPARATION OF NEMATODES

Nematodes were placed in a 10% solution of glycerol in absolute alcohol in a Syracuse watchglass. The watch-glass was covered with a glass plate permitting the ethanol to evaporate slowly during three to four weeks, leaving pure glycerol. Excellent results were obtained by this method.

TISSUE SECTIONS

Tissues were embedded in Paraplast and sections cut of 6-10 micra. These sections were stained with either Mallory's Triple Stain, Ehrlich's or Heidenhain's haema-toxylin.

IDENTIFICATION OF HELMINTHS

Helminths were identified using the Zoology of Tapeworms (108), the Nematode Parasites of Vertebrates (112), original literature and drawings, and comparative specimens.

TABULATION OF DATA

The species, sex, age of reach rodent and the presence and position of any helminths were recorded in a field manual and then transferred to a data sheet (Fig.4).

Figure 4. Data tabulation sheet.

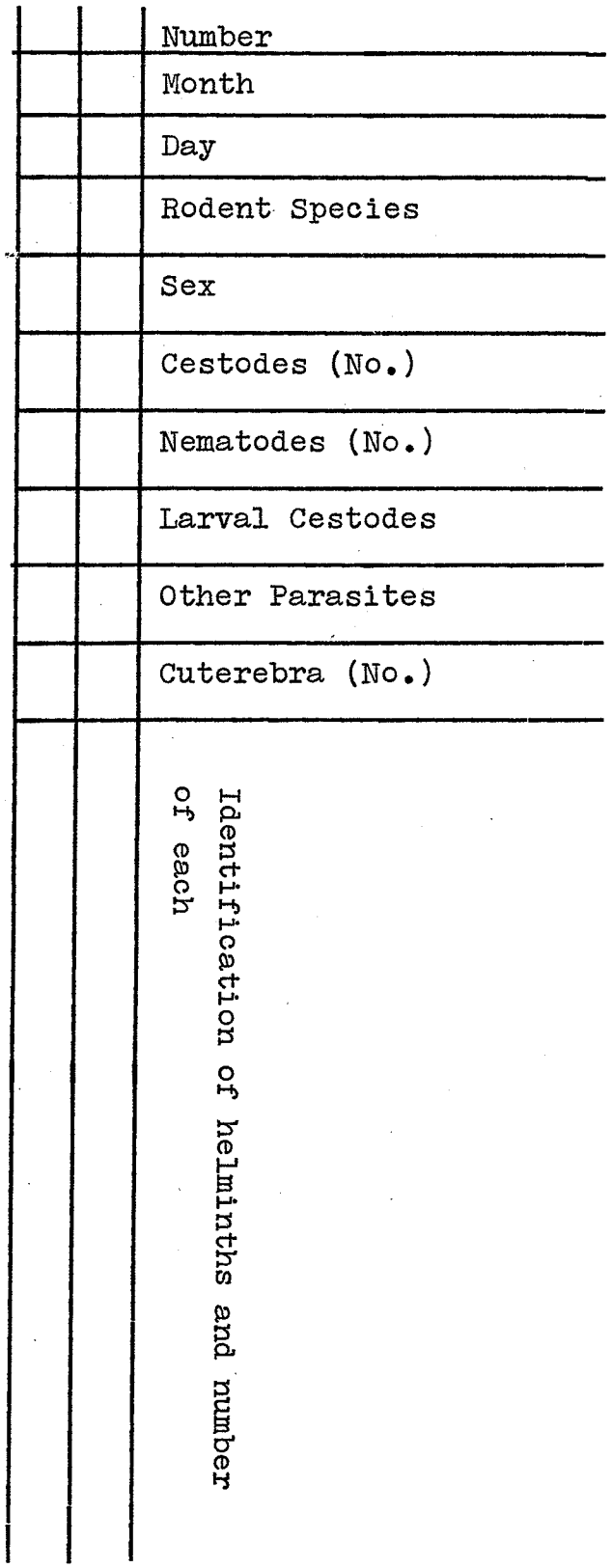

Number
Month
Day
Rodent Species
Sex
Cestodes (No.)
Nematodes (No.)
Larval Cestodes
Other Parasites
Cuterebra (No.)
Identification of helminths and number of each

Figure 4.

TABLE III

LIST OF HOSTS AND OF THEIR HELMINTHS

RODENTIA

Family Cricetidae

Subfamily Cricetinae

1) Peromyscus maniculatus bairdi (Hoy and Kennicott)

Capillaria hepatica (Bancroft, 1896)

Subfamily Microtinae

2) Microtus pennsylvanicus drummondi (Audubon and Bachman)

Andrya bairdi Schad, 1954

A. macrocephala Douthitt, 1915

Paranoplocephala infrequens (Douthitt,1915)

P. variabilis (Douthitt,1915)

Hydatigera taeniaeformis (Batsch, 1786)

Taenia mustelae Gmelin, 1790

Capillaria hepatica (Bancroft, 1896)

Heligmosomum costellatum (Dujardin,1845)

H. microti (Kuns and Rausch, 1950)

Syphacia obvelata (Rudolphi, 1802)

3) Clethrionomys gapperi gapperi (Vigors)

Andrya bairdi Schad, 1954

A. macrocephala Douthitt, 1915

Catenotaenia dendritica (Goeze, 1782)

Taenia mustelae Gmelin, 1790

Capillaria hepatica (Bancroft, 1786)

Heligmosomum microti (Kuns and Rausch, 1950)

Syphacia obvelata (Rudolphi, 1802)

TABLE III (continued)

4) Clethrionomys gapperi loringi (Bailey)

Andrya macrocephala Douthitt, 1915

Catenotaenia dendritica (Goeze, 1782)

Taenia mustelae Gmelin, 1790

NOTES ON THE BIOLOGY OF THE HOSTS

One thousand and sicty-one rodents of five species (eight subspecies) were examined. The following section gives brief notes on each of these rodent species. The parasites of each host are listed in Tables III and IV. Additional findings on Peromyscus maniculatus bairdi are given in Appendix I.

Cricetidae

Peromyscus maniculatus (Wagner, 1945) Deer Mouse

Two subspecies of this rodent were found in southern Manitoba: Peromyscus maniculatus maniculatus (Wagner) at Pinawa, and Peromyscus maniculatus bairdi (Hoy and Kennicott) at Delta and in the disturbed grassland area (its typical habitat) of Winnipeg and western Manitoba. Both subspecies were restricted to treed biotopes or to fields bordering on groves of poplar.

Specimens of P. maniculatus trapped in this survey were free of intestinal parasites (see Appendix I), but 3 out of 24 specimens taken in the lakeshore forest were infected with the liver parasite, Capillaria hepatica. Schad (89) also did not find intestinal parasites in Peromyscus from northeastern Quebec and Labrador, but found nematodes in Peromyscus from the MacDonald College Arboretum in southern Quebec. Lubinsky (65) and Freeman and Wright (35) found C. hepatica in P. maniculatus in Alberta and in Algonquin Park, Ontario, respectively. It is not clear why intestinal parasites are so scarce in this host.

Microtus pennsylvanicus drummondi (Audubon and Bachman,1854)

Commonly called Drummond's meadow vole, this rodent was numerous in open fields,and rare in wooded areas.

Ten species of helminths were found in 23.4% of M. p. drummondi (Fig.5). The most frequent cestodes infecting this host were Taenia mustelae (9.7%) and Andrya macrocephala (9.1%). Syphacia obvelata and Heligmosomum microti were the most frequent nematodes (2.0%). Seven out of 465 specimens of M. p. drummondi from the Winnipeg area were infected with one to seven cysts of Hydatigera taeniaeformis. Four of 14 specimens from the lakeshore forest at Delta were infected with Capillaria hepatica.

The findings of Andrya bairdi (0.5%), Capillaria hepatica (0.6%), and Heligmosomum costellatum (0.3%) in M. p. drummondi are new host records.

Clethrionomys gapperi (Vigors, 1830)

Two subspecies of the red back vole were examined: Clethrionomys gapperi gapperi (Vigors) at Pinawa, and Clethrionomys gapperi loringi (Bailey) at Delta and Winnipeg.

Three species of cestodes were found in C. g. gapperi from Pinawa: Andrya macrocephala, Catenotaenia dendritica, and Taenia mustelae; no nematodes were found. These three cestodes along with Andrya bairdi were found in C. g. loringi at Delta, as were the nematodes Capillaria hepatica, Heligmosomum microti, and Syphacia obvelata.

The findings of Andrya bairdi, Capillaria hepatica,and Heligmosomum microti in C. g. loringi are new host records.

Figure 5. Percentage infection of Microtus pennsylvanicus drummondi with helminths in Manitoba.

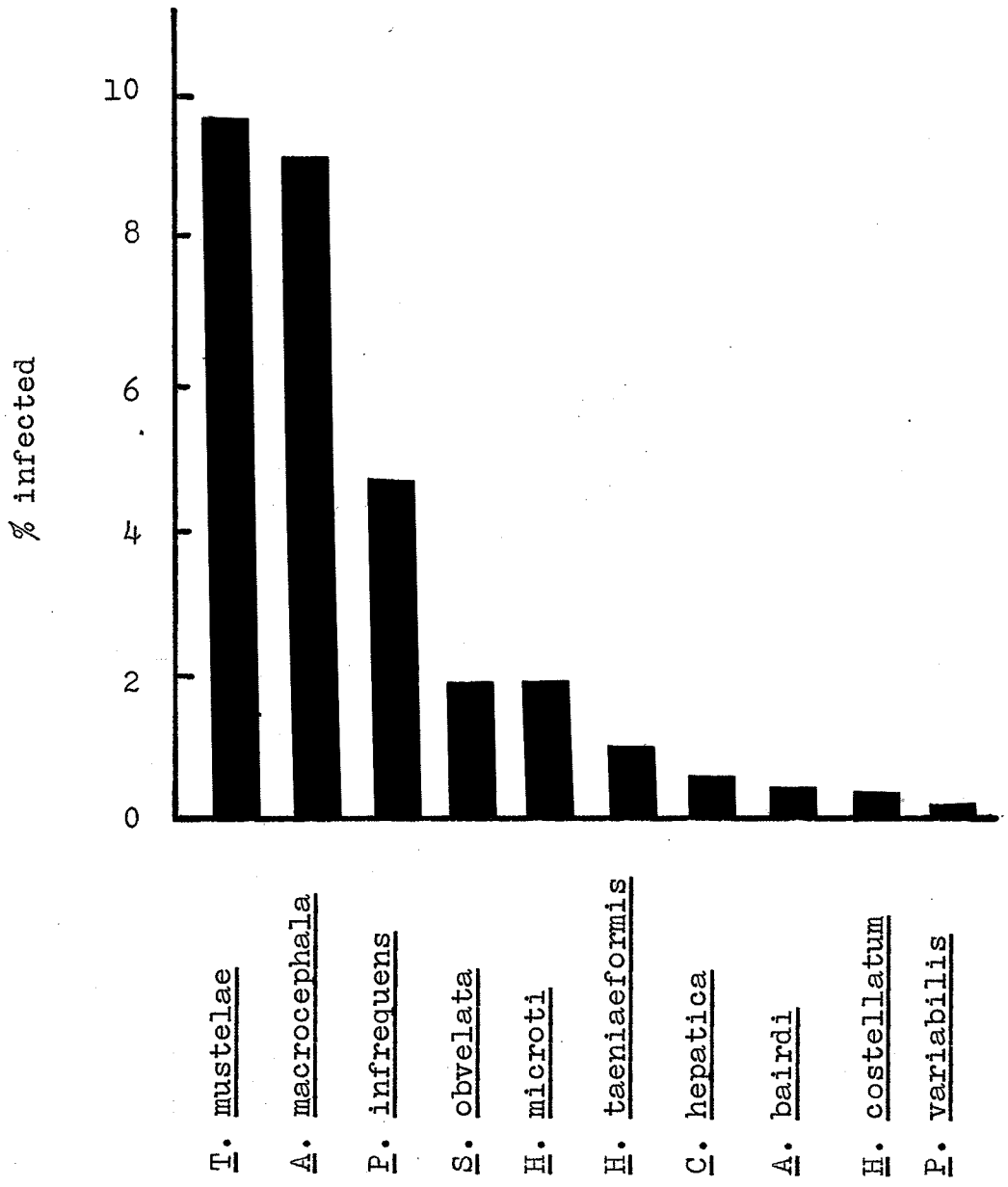

% infected
10
8
6
4
2
0
T. mustelae
A. macrocephala
P. infrequens
S. obvelata
H. microti
H. taeniaeformis
C. hepatica
A. bairdi
H. costellatum
P. variabilis

Figure 5.

Zapodidae

Zapus hudsonius (Zimmermann, 1780)

Zapus hudsonius hudsonius (Zimmermann) was taken at Pinawa in open fields and aspen-ash forest, Zapus hudsonius campestris (Preble) at Delta in the marsh and lakeshore forest. All ten specimens collected were free of parasites. Erickson (29) found two species of nematodes in the intestine of Z. hudsonius. Freeman and Wright (35) found Capillaria hepatica and larval Taenia mustelae in the liver of this rodent.

Napeozapus insignis frutectanus (Jackson)

Only one specimen of this rare rodent was taken from an aspen grove at Pinawa. It was free of parasites. Freeman and Wright (35) found one infection of N. insignis with Capillaria hepatica in Algonquin Park, Ontario.

TABLE IV

LIST OF HELMINTHS FOUND

CESTODA

Order Cyclophyllidea Braun, 1900

Family Anoplocephalidae Cholodkovsky, 1902

Subfamily Anoplocephalinae Blanchard, 1891

1) Andrya bairdi Schad, 1954

Clethrionomys gapperi loringi - small intestine; Delta. New host record.

Microtus pennsylvanicus drummondi - small intestine; Winnipeg. New host record.

2) Andrya macrocephala Douthitt, 1915

Clethrionomys gapperi gapperi - small intestine; Pinawa.

Clethrionomys gapperi loringi - small intestine; Delta.

Microtus pennyslvanicus drummondi - small intestine; Delta, Pinawa, Winnipeg.

3) Paranoplocephala infrequens (Douthitt, 1915)

Microtus pennsylvanicus drummondi - ileocaecal junction and caecum; Winnipeg.

4) Paranoplocephala variabilis (Douthitt, 1915)

Microtus pennsylvanicus drummondi - ileocaecal junction and caecum; Winnipeg.

Family Catenotaeniidae Wardle and McLeod, 1952

5) Catenotaenia dendritica (Goeze, 1782)

Clethrionomys gapperi gapperi - small intestine; Pinawa.

Clethrionomys gapperi loringi - small intestine; Delta.

TABLE IV (continued)

Family Taeniidae Ludwig, 1886

6) Hydatigera taeniaeformis (Batsch, 1786) (larvae)

Microtus pennsylvanicus drummondi - liver; Winnipeg.

7) Taenia mustelae Gmelin, 1790 (larvae)

Clethrionomys gapperi gapperi - liver; Pinawa.

Clethrionomys gapperi loringi - liver; Delta.

Microtus pennsylvanicus drummondi - liver; Delta, Pinawa, Winnipeg.

NEMATODA

Order Eunematoda Ward, 1916

Superfamily Trichuroidea Railliet, 1916

Family Trichuridae Railliet, 1915

Subfamily Capillariinae Railliet, 1915

8) Capillaria hepatica (Bancroft, 1896)

Clethrionomys gapperi loringi - liver; Delta.

Microtus pennsylvanicus drummondi - liver: Delta. New host record.

Peromyscus maniculatus bairdi - liver; Delta.

Superfamily Strongyloidea Weinland, 1858

Family Trichostrongylidae Leiper, 1912

Subfamily Heligmosominae Travassos, 1914

9½ Heligmosomum costellatum (Dujardin, 1845)

Microtus pennsylvanicus drummondi - small intestine; Pinawa. New host record.

TABLE IV (continued)

10) Heligmosomum microti (Kuns and Rausch, 1950)

Clethrionomys gapperi loringi - duodenum; Delta.

New host record.

Superfamily Oxyuroidea Railliet, 1916

Family Oxyuridae Cobbold, 1864

Subfamily Syphaciinae Railliet, 1916

11) Syphacia obvelata (Rudolphi, 1802)

Clethrionomys gapperi loringi - caecum; Delta.

Microtus pennsylvanicus drummondi - caecum; Emerson and Winnipeg.

Figure 6. Composite diagram of a vole's digestive tract, showing the position of helminths.

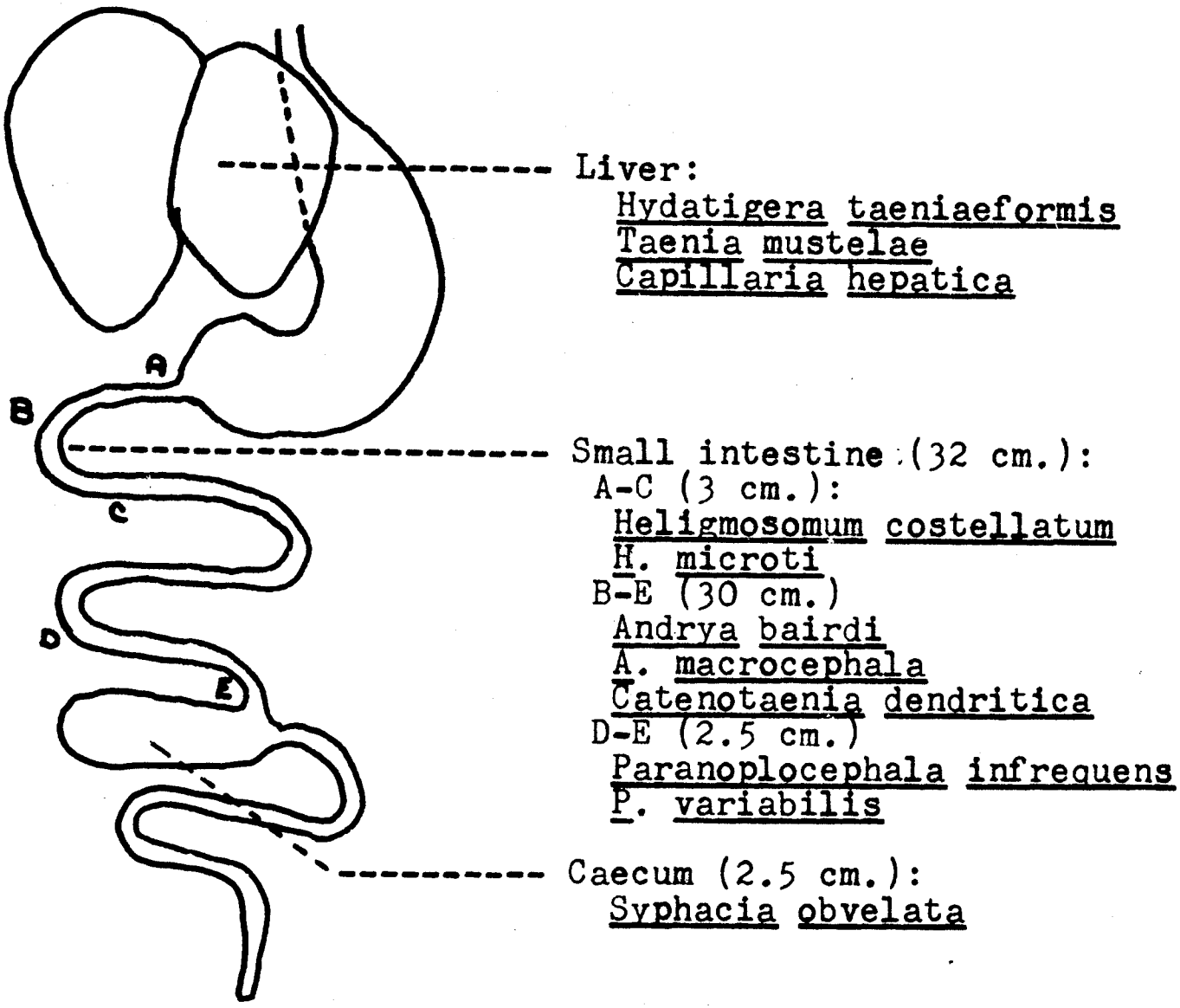

A
B
C
D
E
Liver:
Hydatigera taeniaeformis
Taenia mustelae
Capillaria hepatica
Small intestine (32 cm.):
A-C (3 cm.):
Heligmosomum costellatum
H. microti
B-E (30 cm.)
Andrya bairdi
A. macrocephala
Catenotaenia dendritica
D-E (2.5 cm.)
Paranoplocephala infrequens
P. variabilis
Caecum (2.5 cm.):
Syphacia obvelata

Figure 6.

TABLE V

Helminth Parasites of Rodents from Various Biotopes in Southern Manitoba

Parasite and Host	AREA I Disturbed Grassland			AREA II Lakeshore Forest			AREA III Backshore Marsh			AREA IV Open Fields			AREA V Aspen-Ash Forest		
	% inf.	of	N	% inf.	of	N	% inf.	of	N	% inf.	of	N	% inf.	of	N
Cestodes															
Andrya bairdi															
M. p. drummondi	0.7± 0.4%*		465	—			—			—			—		
C. g. loringi	—			2.6± 1.1%		216	—			—			—		
A. macrocephala															
M. p. drummondi	9.3± 1.4%		465	25.0±11.6%		14	12.8± 3.0%		125	6.8± 2.3%		117	33.3±27.2%		3
C. g. gapperi	—			12.9± 2.3%		216	—			—			—		
C. g. loringi	—			—			—			—			25.4± 5.8%		56
Paranoplocephala infrequens															
M. p. drummondi	7.3± 1.2%		465	—			—			—			—		
P. variabilis															
M. p. drummondi	0.2± 0.2%		465	—			—			—			—		
Catenotaenia dendritica															
C. g. gapperi	—			—			—			—			1.7± 1.7%		56
C. g. loringi	—			1.9± 0.9%		216	—			—			—		
Hydatigera taeniaeformis															
M. p. drummondi	1.5± 0.6%		465	—			—			—			—		
Taenia mustelae															
M. p. drummondi	9.0± 1.3%		465	—			18.7± 3.5%		125	4.3± 1.9%		117	—		
C. g. gapperi	—			—			—			—			3.4± 2.4%		56
C. g. loringi	—			1.9± 0.9%		216	—			—			—		
Nematodes															
Capillaria hepatica															
M. p. drummondi	—			28.6±12.1%		14	—			—			—		
C. g. loringi	—			47.5± 3.4%		216	—			—			—		
P. m. bairdi	—			12.5± 6.8%		24	—			—			—		
Heligmosomum costellatum															
M. p. drummondi	—			—			—			1.7± 1.2%		117	—		
H. microti															
M. p. drummondi	—			—			10.6± 2.8%		125	—			—		
C. g. loringi	—			0.9± 0.6%		216	—			—			—		
Syphacia obvelata															
M. p. drummondi	2.4± 0.7%		465	—			—			—			—		
C. g. loringi	—			1.9± 0.9%		216	—			—			—		

*Standard error = $\sqrt{\frac{100(100 - \%\ \text{inf.})}{N}}$

NOTES ON THE PARASITES FOUND

Eleven species of helminths infected the rodents examined: seven of cestodes and four of nematodes. In this chapter will be discussed my findings, previous findings in North America, and the taxonomy of each parasite. (The position of each parasite in the host is given in Fig. 6)

CESTODA

1. *Andrya bairdi* Schad, 1954

Findings in southern Manitoba:

Winnipeg: *M. pennsylvanicus*	3 of 465 (0.7%)
Delta: *C. gapperi loringi*	3 of 117 (2.6%)
No. of individuals per host:	1
Location in host:	small intestine

A. bairdi was described from *M. chrotorrhinus* in northern Quebec (89) but has not been reported since. The findings of *A. bairdi* in *M. pennsylvanicus* and *C. gapperi* are therefore new host records.

A. bairdi is similar to *Andrya primordialis* Douthitt, 1915 in having unilaterally arranged genital pores, but it lacks the prostate gland which was described in the latter species by Douthitt. Rausch (80) saw a prostate gland in *A. primordialis*. *A. bairdi* may be a junior synonym of *A. primordialis* as Douthitt (23) may have mistaken an enlarged external seminal vesicle for the prostate gland. In my material this vesicle was often greatly distended with sperm or looped over itself, and could be

mistaken for a prostate gland. An examination of many specimens of both species is necessary to solve this problem.

2. Andrya macrocephala Douthitt, 1915

Findings in southern Manitoba:

Winnipeg:	M. pennsylvanicus	43 of 465 (9.3%)
Delta:	C. g. loringi	28 of 216 (12.9%)
Pinawa:	C. g. gapperi	14 of 58 (23.3%)
	M. pennsylvanicus	7 of 120 (7.5%)
No. of individuals per host:		1 - 13
Location in host:		small intestine

A. macrocephala is the most common cestode of microtine rodents in North America. Its high morphological variability has led to the description of several species with overlapping characteristics (Rausch and Schiller (84), Rausch (80)). The type host of A. macrocephala is Geomys bursarius. In 1915, Douthitt (23) described A. translucida from the same host. Kirshenblat (52) described A. caucasica from Microtus socialis and Cricetulus migratorius in Transcaucasia.

Kirschenblatt subdivided the genus Andrya into two subgenera: Andrya and Apostandrya, placing in the latter the species A. macrocephala, A. translucida and A. caucasica.

In 1947, Hansen (44) described A. microti from M. ochrogaster; in 1948, Rausch (77) described A. ondatrae from Ondatra zibethicus; and Soltys (99) described

Figure 7. Mature segment of a sterile *Andrya macrocephala*.

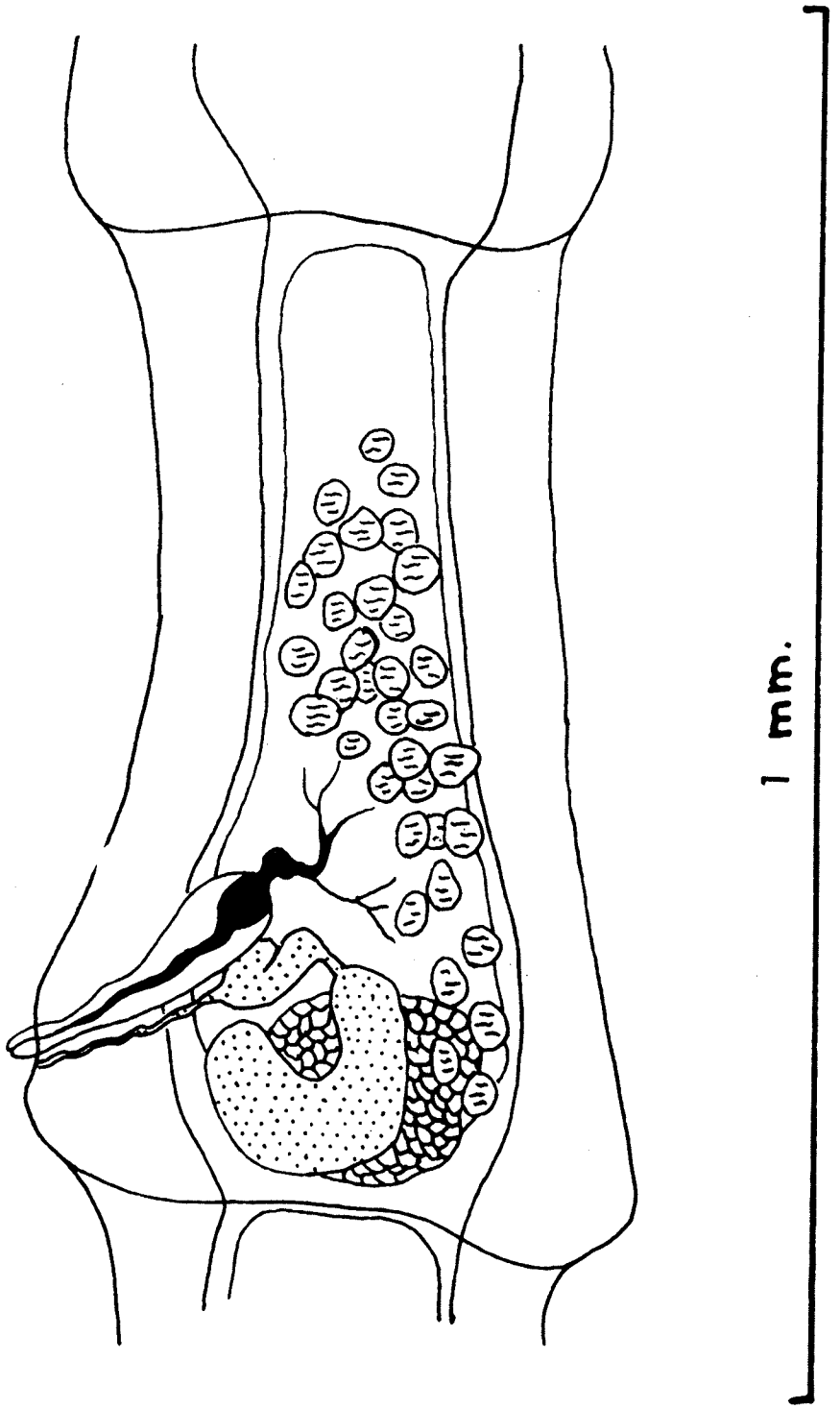


Figure 7.

A. bialowiezensis from Microtus arvalis in Poland.

Rausch and Schiller (84) regarded A. microti, A. ondatrae, and A. caucasica as junior synonyms of A. macrocephala. Rausch (82) in 1957 showed that A. bialowizensis is morphologically identical with A. macrocephala and added it to the list of synonyms of A. macrocephala. Rausch and Schiller (84) found that certain individuals of A. macrocephala are sterile and their proglottids become elongated due to the absence of ova (Fig.7). This can be explained by the following: the uterus of A. macrocephala is a transverse sac; when it is full of eggs it exerts a lateral pressure and the proglottids become wide and short. When the proglottid is sterile, no lateral pressure is exerted and it becomes elongated.

Two specimens of A. macrocephala in one M. pennsylvanicus extended into the stomach. This may have been due to movement of the worms after death of the host or to antiperistalsis in the moribund animals.

3. Paranoplocephala infrequens Douthitt, 1915

Findings in southern Manitoba:

Winnipeg:	M. pennsylvanicus	34 of 465 (7.3%)
No. of individuals per host:		1 - 7
Location in host:	ileocaecal junction and caecum	

In the present survey P. infrequens was found only in the greater Winnipeg area, and only in M. pennsylvanicus.

Anoplocephala infrequens, A. variabilis, and A. varia-

bilis borealis were described by Douthitt in 1915 from Geomys bursarius in Minnesota (23). He also recorded A. variabilis from Evotomys (Clethrionomys) in North Dakota. In 1927, Baer (4) placed the above three species in the genus Paranoplocephala, and at the same time synonymized P. variabilis with P. infrequens. Rausch (76) described P. troeschi from M. pennsylvanicus in Michigan and Ohio in 1946. (Rausch gave two type localities for this cestode.) In 1947, Hansen (44) reestablished P. variabilis as a valid species on the basis of a skirt-like projection of the posterior margin of the proglottids of P. infrequens. Rausch and Schiller (84) regarded P. troeschi as a junior synonym of P. infrequens and raised P. variabilis borealis to full specific rank as P. borealis. Rausch (80) reassessed the position of P. borealis and concluded, in 1952, that it was "only a stage in the growth of P. variabilis".

4. Paranoplocephala variabilis Douthitt, 1915

Findings in southern Manitoba:

Winnipeg: M. pennsylvanicus	1 of 465 (0.2%)
No. of individuals per host:	1
Location in host:	ileocaecal junction

The taxonomic position of P. variabilis was already discussed in the section dealing with P. infrequens. P. variabilis showed the same peculiarities with regard to localities, hosts, and location in the host. Rausch (80) showed in 1952 that P. variabilis varies considerably in size with age. Unfortunately, my material was insufficient

for the study of this variability.

P. variabilis was reported from hosts other than Microtus: Synaptomys cooperi from southern Illinois (80), Thomomys talpoides from Michigan (80) and Alberta (65), Dicrostonyx hudsonius from Labrador and northeastern Quebec (89), and Phenacomyx intermedius from Alberta (65).

5. Catenotaenia dendritica Goeze, 1782

Findings in southern Manitoba:

Delta:	C. gapperi loringi	4 of 216 (1.9%)
Pinawa:	C. g. gapperi	1 of 58 (1.7%)
No. of individuals per host:		1 - 6
Location in host:		small intestine

This cestode was found only in Clethrionomys gapperi. Table VII shows that C. dendritica is to some extent specific for this host, though it was reported from Peromyscus maniculatus by Leiby (58) from Idaho in 1962 (see also Appendix I). This parasite is rare (81), but may occur frequently in some foci, as shown by Schad (89).

Catenotaenia dendritica was described from Sciurus vulgaris in Europe (38). In 1941, McIntosh (69) described C. linsdalei from California pocket mice and kangaroo rats (69). Schad (89), after comparing measurements given by Joyeux and Baer (48), Yamaguti (111), McIntosh (69), and Voge (105) concluded that C. linsdalei McIntosh is a junior synonym of C. dendritica Goeze.

C. dendritica exhibits considerable morphological variation. Rausch (79) stated that "in various anoplocephaline genera, including Catenotaenia, the lack of

constant characters, for example rostellar hooks, makes it necessary to pay particular attention to variation when specific differentiation is attempted. In Catenotaenia it would seem advisable to consider the state of strobilar contraction, as the relative position of organs are often greatly influenced by this. Any lot of material consisting of strobilae either uniformly contracted or relaxed could convey an impression which might lead to an erroneous conclusion in regard to specific characterization". Differences in morphology caused by contraction or relaxation of the cestode may also account for the wide morphological variation reported in Andrya macrocephala.

6. Hydatigera taeniaeformis (Batsch, 1786)

Findings in southern Manitoba:

Winnipeg: M. pennsylvanicus drummondi	7 of 465 (1.5%)
No. of individuals per host:	1 - 7
Location in host:	liver

Hydatigera taeniaeformis is a cosmopolitan parasite frequently found near human habitation. The adult worm parasitizes house cats, feral cats, and mustelids. The larva is found in the liver and in the mesenteries of rodents, and seldom in the spleen (101). It is a strobilocercus enclosed in a large, yellowish cyst, 10 to 15 millimetres in diameter. It becomes infective after sixty days of growth.

The occurrence of H. taeniaeformis in North American rodents is summarized in Table VI.

TABLE VI

Records of *Hydatigera taeniaeformis* (Batsch, 1786) in North American rodents

HOST	DATE	AUTHOR	LOCALITY
Mus musculus	1909	McCoy (68)	California
	1919	Hall (42)	"United States"
	1936	Harkema (45)	N. Carolina
	1954	Hall and Sonnenberg (43)	Maryland
	1957	Lubinsky (65)	Alberta
	1963	Lubinsky *	Manitoba
Rattus norvegicus	1919	Hall (loccit) (42)	"United States"
	1936	Harkema (45)	N. Carolina
	1954	Hall and Sonnenberg (43)	Kentucky
Ondatra zibethicus	1932	Law and Kennedy (57)	Ontario
	1942	Ameel (3)	Michigan
	1949	Edwards (26)	New York
	1951	Knight (53)	British Columbia
	1958	Lubinsky *	Quebec (Ile Perrot)
Microtus pennsylvanicus	1938	Erickson (29)	Minnesota
	1949	Rausch and Tiner (85)	North Central States
	1967	Kinsella (51)	Montana
Sciurus carolinensis	1936	Harkema	N. Carolina
S. niger	1934	Dobrovsky and Harbough (21)	Kansas
	1930	Martin (67)	Nebraska

* personal communication

7. Taenia mustelae Gmelin, 1790

Findings in southern Manitoba:

Winnipeg:	M. pennsylvanicus	42 of 465 (9.0%)
Delta:	C. g. loringi	4 of 216 (1.8%)
	M. pennsylvanicus	23 of 139 (16.6%)
Pinawa:	C. g. gapperi	2 of 58 (3.3%)
	M. pennsylvanicus	5 of 120 (4.2%)
Location in host:		liver

Goeze (38), in 1782, found a delicate tapeworm in the brown weasel, but did not name it. He also found tapeworms in the ferret and marten. Gmelin (36), in 1790, on the basis of Goeze's description established a new species, Taenia mustelae, and regarded the cestodes from the weasel (Mustela vulgaris), ferret (Mustela putorius), and the marten (Mustela martis) as cospecific. In 1803, Zeder (113) established a new genus, Halysis, with type species of H. mustelae, and assumed that the cestodes from the marten and ferret were separate species, naming them H. martis and H. putorii.

Rudolphi (87) described in 1810 as "armed cestode", Taenia intermedia from "Mustela Martis" and stated that this species has large hooks. He regarded Gmelin's description of T. mustelae as insufficient, but thought that Gmelin's cestodes may have been identical to his T. intermedia. He also regarded as "species dubiae" T. putorii (H.putorii) and "T. Mustelae vulgaris".

Nine years later, in 1819, in his "Entozoorum synopsis", Rudolphi (88) summarized the literature on

T. intermedia and on unarmed cestodes from mustelids, and described Taenia brevicollis from Mustela erminea, and T. tenuicollis from "Mustela Putorii" and "Mustela Vulgaris". Thus, Rudolphi believed that at least three species of cestodes occurred in mustelids, one with rostellar hooks, and two unarmed.

Küchenmeister in 1955 (54), found in mice an unarmed larval tapeworm which he named Cysticercus innominatus hypudaei. In 1856, Leuckart (61) pointed out that this was probably the larva of T. tenuicollis of mustelids. Two years later, Küchenmeister (55) found this cysticercus in the liver of Talpa europaea, and showed that Cysticercus talpae, Rudolphi 1819, a dubious species from the same host, and believed to be hookless by Rudolphi, had hooks and was probably identical to C. innominatus hypudaei, Küchenmeister 1855.

In 1910, Thienemann (103) reexamined Rudolphi's type specimens of adult cestodes from mustelids in the Vienna Museum, and agreed with Küchenmeister (55) and Leuckart (61) that T. intermedia has relatively large and characteristic hooks, and is readily distinguishable from both T. tenuicollis and T. brevicollis. Thienemann also studied Rudolphi's type specimens of Cystercercus talpae and noted their similarity to adult T. tenuicollis Rudolphi, 1819 and T. brevicollis Rud., 1819. Baer (5), Cameron and Parnell (17), and Joyeux and Baer (48) regarded T. brevicollis as a junior synonym of T. tenuicollis. The fact that the

hooks of T. tenuicollis drop off easily had led to the opinion that this species was unarmed. Therefore, Joyeux and Baer (48), in 1934, regarded an armed cestode which they found in weasels as a new subspecies, T. tenuicollis var. armata.

In 1810, Rudolphi described a larval cestode from cattle which he named Cysticercus tenuicollis. Hughes (47), in 1941, pointed out that the specific name of T. tenuicollis Rud. 1819 is pre-occupied by Cysticercus tenuicollis, Red. 1810, and proposed therefore for T. tenuicollis a new name - Taenia joyeuxiana. In 1956, Freeman (34) reviewed the literature on cestodes from mustelids and stated that, according to the laws of priority, the valid name for the small-hooked taeninoid cestode of the European brown weasel is T. mustelae Gmelin, 1790.

Larvae of T. mustelae were first reported from North America by Skinker (97) in 1935 from the liver of Ontario muskrats; she also found the adult worm in mink. In 1942, Ameel (3) found T. mustelae larvae in muskrats from southern and central Michigan. Rausch (80), in 1952, corrected identifications of larvae to T. mustelae which he had previously described as Cladotaenia in Michigan and Alaska (78, 85) and added Clethrionomys rutilus dawsoni, Lemmus trimucronatus alascensis, and Microtus miurus paneaki from Alaska to the list of hosts.

Locker (63) reported larvae of T. mustelae from Microtus oecomomus in Alaska, Ondatra zibethicus osoyoosensis,

M. pennsylvanicus modestus, and Peromyscus maniculatus artemisiae in Montana, the mountain beaver Aplodontia rufa and P. maniculatus rubidus in Oregon. She also found the adult cestodes in Mustela erminea invicta and Mustela vison in Montana.

Freeman (34) examined 1562 rodents from Ontario and Michigan, and found 46 infected with T. mustelae. These were Citellus franklinii, Eutamias minimus, Marmota monax, Tamias striatus, Clethrionomys gapperi, Microtus pennsylvanicus, Peromyscus sp., Peromyscus maniculatus, Synaptomys cooperi, and Zapus hudsonius.

Two larval forms of T. mustelae with different hook lengths infect rodents; these are often called the European and North American varieties. The European variety has hooks with an average length of 20 u. The larvae which Rausch (78,85) at first misidentified as Cladotaenia had hooks either 16 or 20 u long. This was the first report of both types of larvae in North American rodents.

I also found both forms in Manitoba rodents. At Delta, only the European variety was found, while at Pinawa and Winnipeg both varieties were present. The measurements of the larval hooks (Fig.8) were as follows:

A. Larvae with large hooks:

No. of hooks examined:	345 (45 scoleces)
No. of hooks per scolex:	40-56 (mean 46.3)
Mean length:	22.1 $\pm$ 0.1 u

Figure 8. (a) Scolex of a larva of
Taenia mustelae (x 125)
(b) Rostellar hooks of
T. mustelae larva (x 550)

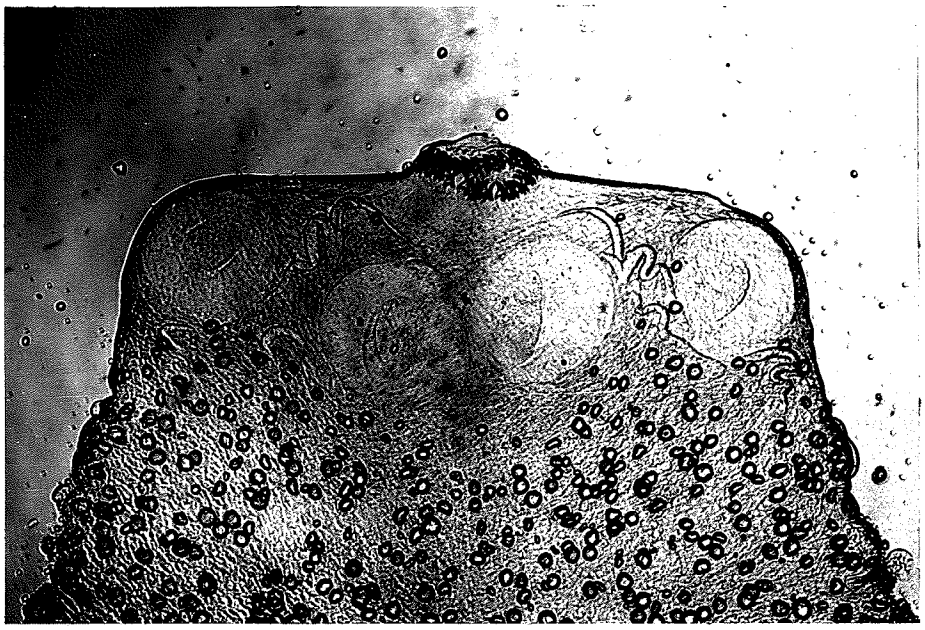


Fig. 8 (a).

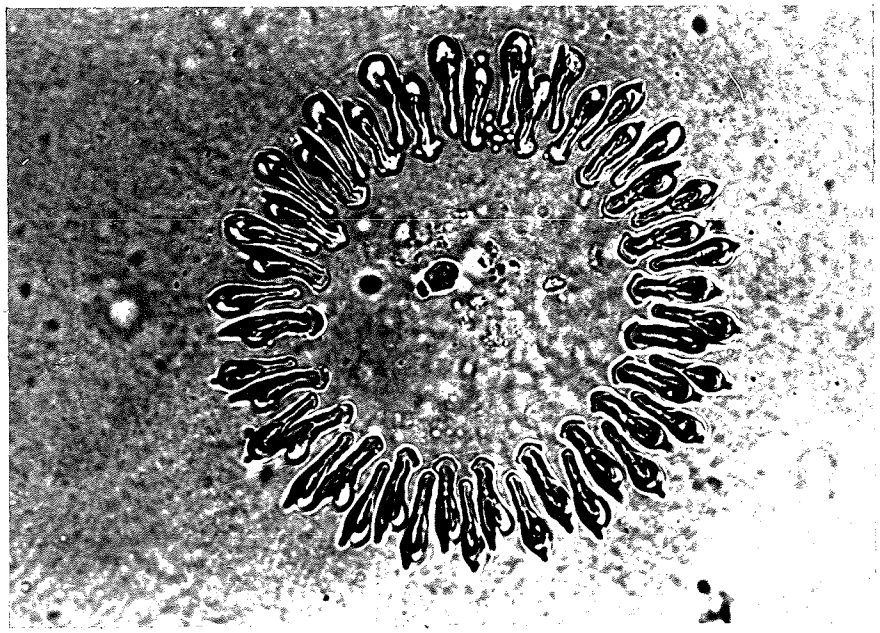


Fig. 8 (b).

Figure 9. Liver of *Microtus pennsylvanicus drummondi* infected with larvae of *Taenia mustelae* (x 2).

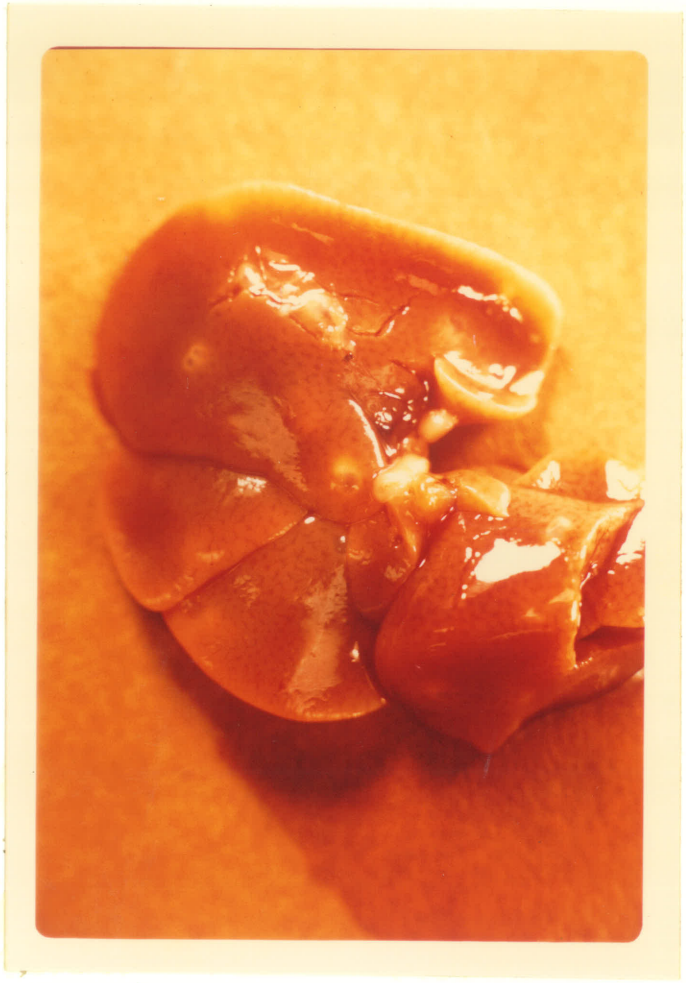


Fig. 9.

B. Larvae with small hooks:

No. of hooks examined: 73 (2 scoleces)

No. of hooks per scolex: 42 and 44

Mean length: 16.6 ± 0.1 u

A z-test showed that in my material no significant difference existed in the hook lengths of the two rows in either form of larvae (z= 0.1542).

An unusual feature of T. mustelae larvae is that the large-hooked variety is a cysticercus (Fig.9) whereas the small-hooked larvae can be either cysticerci or coenuri, i.e. either uniscolex or multiscolex larvae. Previous authors (34, 63, 97) discussed this phenomenon in detail. Freeman (34) found that uniscolex larvae, fed to mink, grew into adults which produced larvae of both types.

Of the seven small-hooked larvae infections, one was uniscolex, six multiscolex. Unfortunately, only two of the coenuri had scoleces with fully-developed hooks.

NEMATODA

8. Capillaria hepatica (Bancroft, 1896)

Findings in southern Manitoba:

Delta:	M. pennsylvanicus	4 of 139 (2.9%)
	C. g. loringi	103 of 218 (47.5%)
	P. maniculatus	3 of 24 (12.5%)

No. of individuals per host: impossible to determine

Location in host: liver

This parasite was discovered in 1896 in the liver

of a rat and named Trichocephalus hepaticus. In 1916, Hall (41) created for it the genus Hepaticola. In 1931, Baylis (8) reexamined the morphology of H. hepatica and showed that its generic characteristics coincide with those of the genus Capillaria, and that the creation of a new genus for it was unjustified.

Firlotte (33) found C. hepatica in brown rats on the campus of Macdonald College, Quebec. Law and Kennedy (57) reported the parasite in muskrats in Ontario. Freeman and Wright (35) found it in Clethrionomys gapperi, Microtus p. pennsylvanicus, Napeozapus insignis algonquinensis, Ondatra zibethicus, Peromyscus maniculatus and Synaptomys c. cooperi.

In Manitoba, C. hepatica was found only in rodents trapped along the Delta sand ridge, and did not occur in those collected in the neighbouring Delta marsh.

Calle (16) recently reported the life cycle of C. hepatica as direct, requiring only a single host whose liver contains both the adult parasites and their ova (Figs.10-13). The cycle starts when the host dies, decomposes, and thus liberates the ova, or when the host is eaten by another animal that passes the undigested ova in the faeces and disseminates them in the soil. Under favourable circumstances the ova embryonate within 30 days, and become infectious. The life cycle is completed when animals or man become infected by ingesting food contaminated with the embryonated ova. Following inges-

Figure 10. Clethrionomys gapperi loringi infected with Capillaria hepatica.

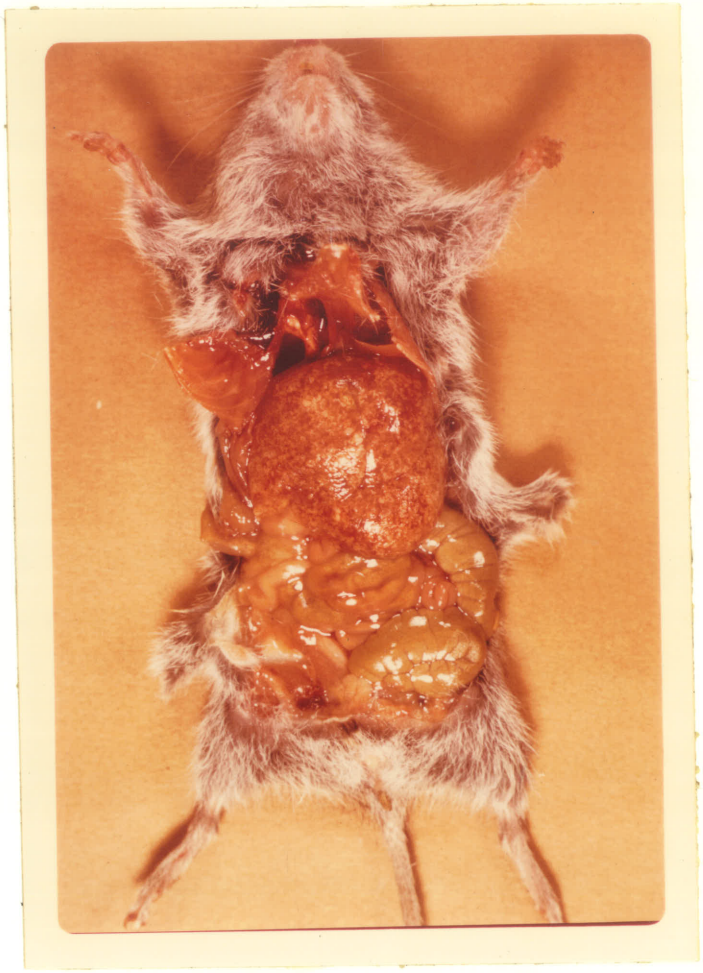


Fig. 10.

Figure 11. Close-up of the infected liver shown in Figure 10 (x 2).

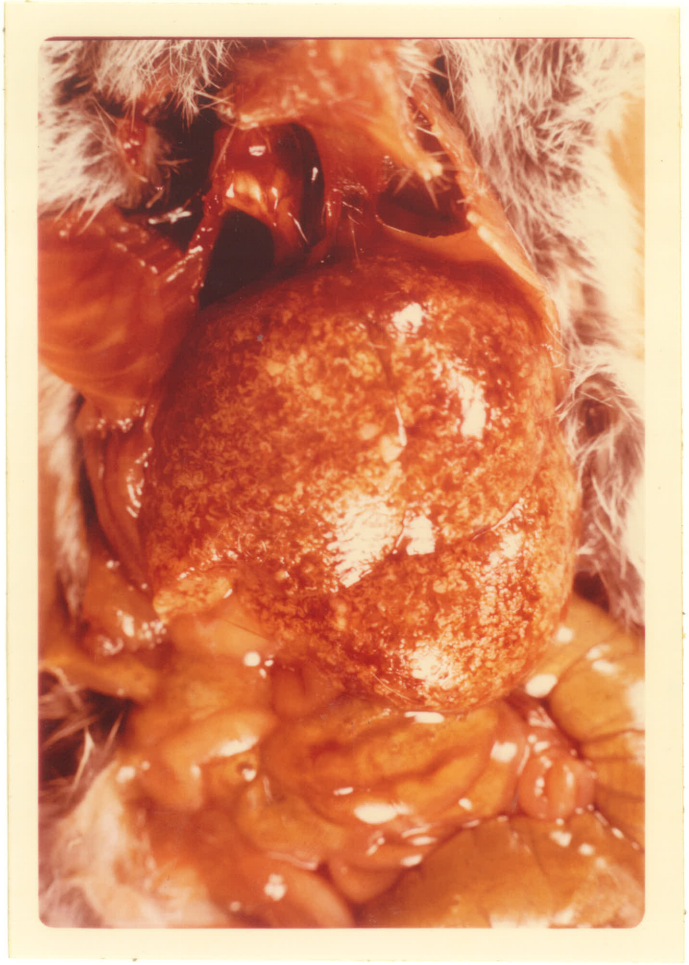


Fig. 11.

Figure 12. Longitudinal section through *Capillaria hepatica* in liver of *Clethrionomys gapperi loringi* (x 100)

Figure 13. Cross-section through *Capillaria hepatica* in liver of *Clethrionomys gapperi loringi* (x 500)

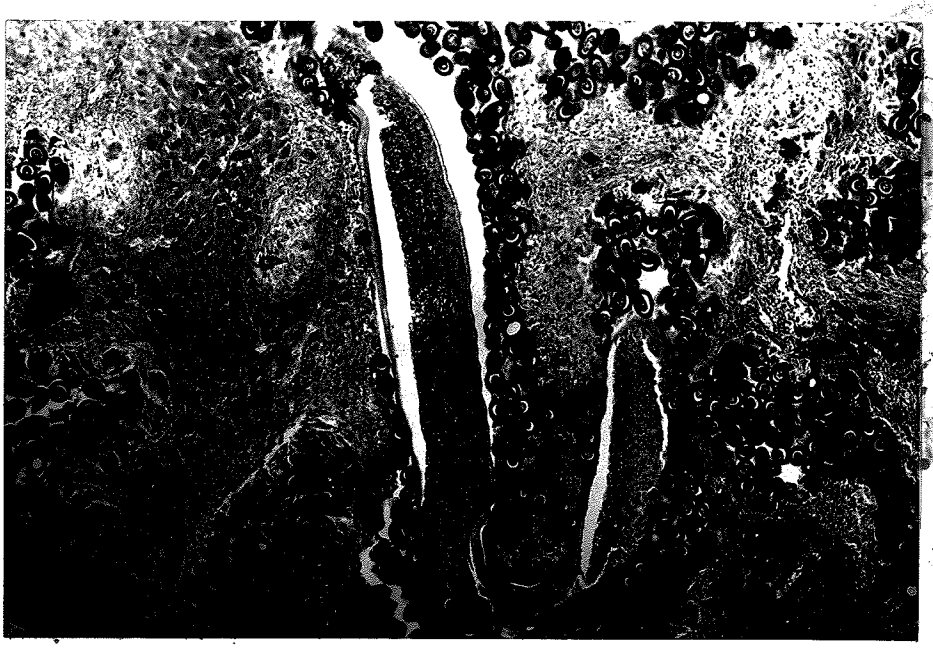


Fig. 12.

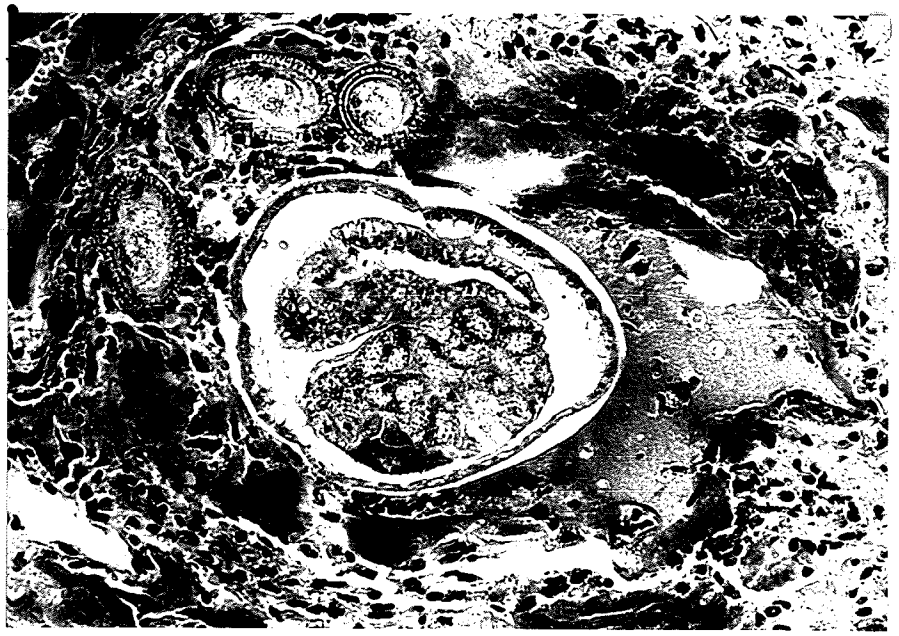


Fig. 13.

tion, the juveniles hatch in the intestine, penetrate into the intestinal wall and migrate to the liver via the portal vein. A few juveniles may pass the portal filter and be carried to the lungs, kidneys or other organs. In the liver, the juveniles mature and mate within approximately one month. Thousands of ova are deposited in the liver and remain there until the death of the host.

According to Freeman and Wright (35), infection takes place in the winter with the release of eggs from the liver due to cannibalism as a result of starvation. Fig. 17 indicates that infection does not take place in the winter but in late July and August in Manitoba. Infections are heavy in the spring (i.e. large numbers of worms), light in mid-summer, and heavy in autumn; I did not find infections of Peromyscus until September, 1967. The intensity of infection may be directly proportional to the number of infected individuals in the rodent population.

Freeman and Wright (35) stated: "The data from Algonquin Park are in marked contrast to those collected by Pavlov in Russia. In 1952 and 1953 he trapped mice from July through September and found a striking rise in the incidence of C. hepatica in the young of the year at the beginning of September. Pavlov concluded that variations in the incidence of this parasite, among the three species of rodents that were infected, were due partly to the

kinds of foods eaten and partly to where they lived since mice living in a flood biotope had a higher incidence than those in a dry biotope... the incidence of Peromyscus maniculatus (in Ontario) varies directly with the density of the host. The eggs must be released from an infected host by cannibalism."

9. Heligmosomum costellatum (Dujardin, 1845)

Findings in southern Manitoba:

Pinawa:	M. pennsylvanicus	2 of 120 (1.7%)
No. of individuals per host:		2 - 4
Location in host:		small intestine

Heligmosomum costellatum is a common parasite of European voles, occurring in all vegetational zones in Europe. In North America it was reported only from Wyoming (56), Alaska (80), and Montana (51). In Wyoming, Kuns and Rausch found this nematode in alpine and subalpine meadows, and not in the lowlands; Kinsella (51) reported H. costellatum from one Microtus longicaudus near Missoula, Montana. Although Kinsella does not describe the biotopes in which he trapped, they lie in the Bitterroot Mountains, and it is probable that this nematode was found in a biotope similar to that reported by Kuns and Rausch.

Erhardova (28) found this parasite in all vegetational zones of the High Tatra Mountains of Czechoslovakia. In the Jeseniky Mountains, Tenora (100) found H. costellatum in the mountain zone; he also found it

in the alpine and subalpine zones of the Liptovske Hole Mountains in Czechoslovakia (101).

In Manitoba, H. costellatum was found only in open fields at Pinawa. The finding of this nematode in Microtus pennsylvanicus drummondi is a new host record.

10. Heligmosomum microti (Kuns and Rausch, 1950)

Findings in southern Manitoba:

Delta:	M. pennsylvanicus	14 of 139 (10.1%)
	C. g. loringi	2 of 216 (0.9%)
No. of individuals per host:		2 - 5
Location in host:		small intestine

Heligmosomum microti was first described from Wyoming voles as Nematospiroides microti (56). It is a small, spirally-coiled, blood-red nematode inhabiting the anterior end of the small intestine. It differs from other species of the genus in the length of its spicules which are 2.08 - 2.20 mm. long. Skrjabin, Shikhobalova, and Shul'ts (98) in 1954, placed Nematospiroides in the genus Heligmosomum. H. microti was not included in the revision of the genus Heligmosomum because of lack of comparative material. N. microti was placed in this genus only in 1967 by Kinsella on the basis of examination of a large material.

In Manitoba, I found H. microti only at Delta. Its finding in Clethrionomys gapperi loringi is a new host record.

11. Syphacia obvelata (Rudolphi, 1802)

Findings in southern Manitoba:

Delta:	C. g. gapperi	4 of 216 (1.9%)
Winnipeg:	M. pennsylvanicus	11 of 465 (2.4%)
Emerson:	M. pennsylvanicus	1 of 1

No. of individuals per host: 1 - 7 (females only)

Location in host: small intestine and caecum

Syphacia obvelata occurs usually in large numbers in a high percentage of rodents. In the United States, this parasite is common; in Canada, it was found only by Schad (89) in northeastern Quebec and Labrador. Schad (90) also found a closely related species, S. peromysci, in 84.2% of Peromyscus maniculatus in southern Quebec. Rausch (80) reported that S. obvelata is a common parasite of microtine rodents in Alaska.

DISCUSSION

Seven species of cestodes and four of nematodes were found in the present survey. Only two of these were presend in all five biotopes: Andrya macrocephala and Taenia mustelae. The other parasites were found in either one or two biotopes. Tables VII and VIII show that in the areas of North America chosen for comparison, 19 species of cestodes and 24 of nematodes have been found in the genera of rodents examined in Manitoba. The parasites found in southern Manitoba have already been reported from one or more areas of Canada and the north-central United States where surveys of this type have been conducted.

The parastie fauna of southern Manitoba rodents has only one unexpected omission, the absence of the cestode Hymenolepis horrida. It will probably be found in Manitoba rodents as it has been reported from several adjacent areas (Table VII).

Foci of infection: focal distributions (i.e. areas with very high frequencies of occurrence of a parasite) were found of the cestodes Paranoplocephala infrequens, P. variabilis, and Hydatigera taeniaeformis; and the nematodes Capillaria hepatica, Heligmosomum costellatum, and H. microti. No foci of other parasites were found.

The intermediate hosts of the two species of Paranoplocephala are unknown and no specific reason can be given

TABLE VII

Cestodes Found in Small Rodents in Canada and the North Central United States

	Manitoba (65)	Alberta	Labrador & N.Quebec (89)	Ontario (34)	Quebec (90)	Idaho (57)	Michigan (85)	Minnesota (29)	Montana (51)	Wyoming (56)
Andrya bairdi	CM	-	M	-	-	-	-	-	-	-
A. macrocephala	CM	CM	CM	-	-	-	M	-	M	M
A. primordialis	-	-	-	-	-	-	-	-	-	M
Catenotaenia dendritica	C	C	C	-	-	P	-	-	C	-
Choanotaenia peromysci	-	P	-	-	-	-	-	-	-	-
C. sp.	-	Z	-	-	-	-	M	-	-	-
Cladotaenia globifera	-	-	-	CP	-	-	M	-	-	-
C. mirsoevi	-	C	-	-	-	-	-	-	-	-
Hydatigera taeniaeformis	M	-	-	-	-	-	M	M	M	-
Hymenolepis evaginata	-	-	-	-	-	-	M	-	-	-
H. fraterna	-	-	-	-	-	-	M	-	-	-
H. horrida	-	C	C	-	-	-	-	-	CM	M
Paranoplocephala infrequens	M	M	M	-	-	-	M	-	M	M
P. variabilis	M	M	M	-	-	-	-	-	M	M
Paruterina rauschi	-	-	-	CP	-	-	-	-	-	-
Taenia mustelae	CM	CM	CMP	CMPZ	P	-	-	-	CM	-

C: Clethrionomys gapperi
M: Microtus spp.
P: Peromyscus maniculatus
Z: Zapus hudsonius

TABLE VIII

Nematodes Found in Small Rodents in Canada and the North Central United States

	Manitoba	Alberta	Ontario	Quebec	Labrador & S. Quebec	Michigan	Minnesota	Montana	Wyoming	Idaho
Aspicularis americana	-	-	-	-	-	-	P	CM	-	-
Capillaria hepatica	CMP	P	CMPZ	-	-	-	-	-	-	-
C. muris-sylvatica	-	-	-	P	-	M	-	-	-	-
Dictyocaulus viviparus	-	-	-	-	-	M	-	-	-	-
Heligmosomum carolinensis	-	-	-	-	C	-	-	-	-	-
H. costellatum	M	-	-	-	-	-	-	M	M	-
H.dubius	-	-	-	-	M	-	-	-	-	-
H. microti	CM	-	-	-	-	-	-	M	M	-
Longistriata dalrymplei	-	-	-	-	-	M	-	-	-	-
Mastophorus muris	-	-	-	-	CZ	M	-	M	-	-
Moniliformis sp.	-	-	-	-	-	-	P	-	-	-
Nippostrongylus sp.	-	-	-	-	-	-	-	-	-	P
Pelodera sp.	-	-	-	-	-	-	-	CM	-	-
Protospirura muris	-	C	-	-	-	-	-	-	-	-
P. numidica	-	-	-	-	-	-	-	-	-	P
Rictularia coloradensis	-	M	-	-	-	-	-	-	-	P
Spiuracerca zapi	-	-	-	-	-	-	Z	-	-	-
Sublura ungulatus	-	-	-	-	-	-	Z	-	-	-
Syphacia obvelata	CM	-	-	-	M	M	M	CM	M	M
S. peromysci	-	-	-	P	-	-	-	-	-	P
S. samorodini	-	-	-	-	-	-	P	-	-	-
Trichuris opaca	-	-	-	-	-	-	M	-	M	-

for the foci of these two parasites in the disturbed grasslands. The finding of Hydatigera taeniaeformis only in the disturbed grasslands of Winnipeg probably is due to the restriction of the definitive host (Felis domesticus) to areas of human habitation.

Nematodes with focal distributions found in this survey have direct life cycles. Local conditions favourable to the survival of infective eggs and larvae strongly influence the occurrence of such parasites (56). Kuns and Rausch (56) found that in the cases of Heligmosomum costellatum and H. microti "permanent dampness and coolness...would perhaps account for better survival of nematode eggs and larvae". Rausch and Tiner (85) found that abundance of vole parasites (both cestodes and nematodes) depends upon moisture. The biotopes where Capillaria hepatica and Heligmosomum were found were damp. The effect of dampness is best illustrated by the two species of Heligmosomum. At Delta, two adjacent biotopes were studied: backshore marsh and lakeshore forest. A statistically higher infection rate for H. microti was found in the marsh than in the forest where drainage was good. Similarly, at Pinawa, H. costellatum was found in voles inhabiting damp fields but not in voles in the adjoining and drier aspen-ash forest. These observations support the opinions expressed by Kuns and Rausch, and Rausch and Tiner.

Seasonal variation: My data show that the frequency of helminth infections of Manitoba rodents varies from month to month, and year to year. This depends upon numerous factors, such as seasonal and annual variations in the density of the host populations, and the life cycles of the parasites.

The high incidence (percentage of infected animals) of helminths during May (Fig. 14) is probably due to a persistance of the previous autumn's infections. The steep fall in June reflects the large numbers of young rodents (uninfected) in the populations studied (Fig. 15). A rise in incidence occurred in July, 1966 and a plateau in July, 1967, when the first young rodents became infected. The drop in incidence in mid-summer is probably caused by the great proportion of young in rodent populations at this time of the year. These young became infected in late summer, as shown by the abrupt rise of the curve in August-September.

If sampling were carried out during the winter, the highest incidence probably would be found in the period November to April. Elton, Ford and Baker (27), in 1931, studied infections with Heligmosomum dubium of Apodemus sylvaticus, the Old World counterpart of Peromyscus. They found a peak in the first quarter of the year, and a low in the third quarter. My results resemble those of Elton, Ford, and Baker.

Seasonal variation in rodent parasitism has not been

Figure 14. Seasonal variations in incidence in helminth infections in Clethrionomys, Microtus, and Peromyscus in Manitoba during 1966 and 1967.

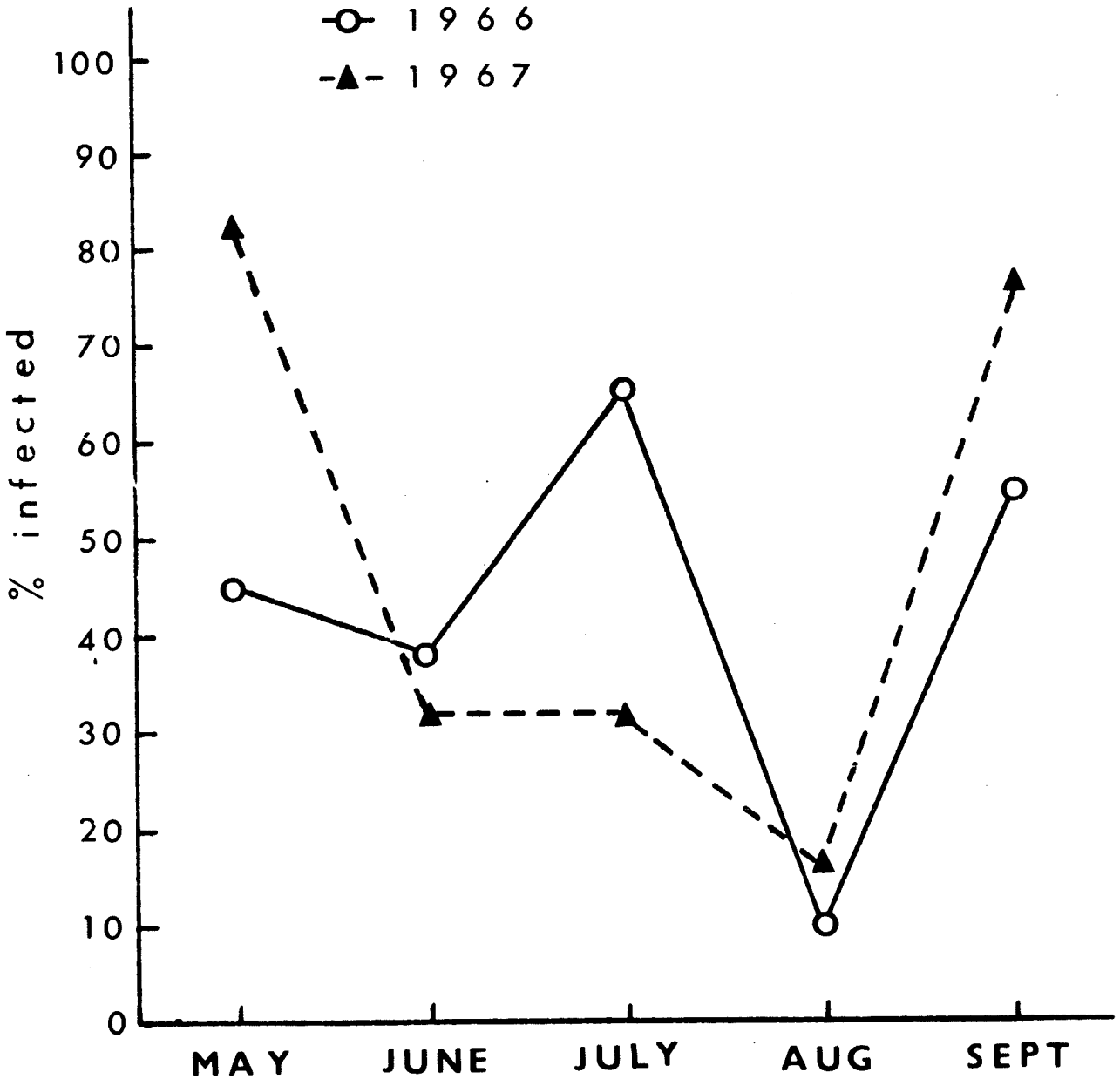

1966
1967
100
90
80
70
60
50
40
30
20
10
0
% infected
MAY
JUNE
JULY
AUG
SEPT

Figure 14.

Figure 15. Proportion of adults in rodent populations from southern Manitoba in 1967.

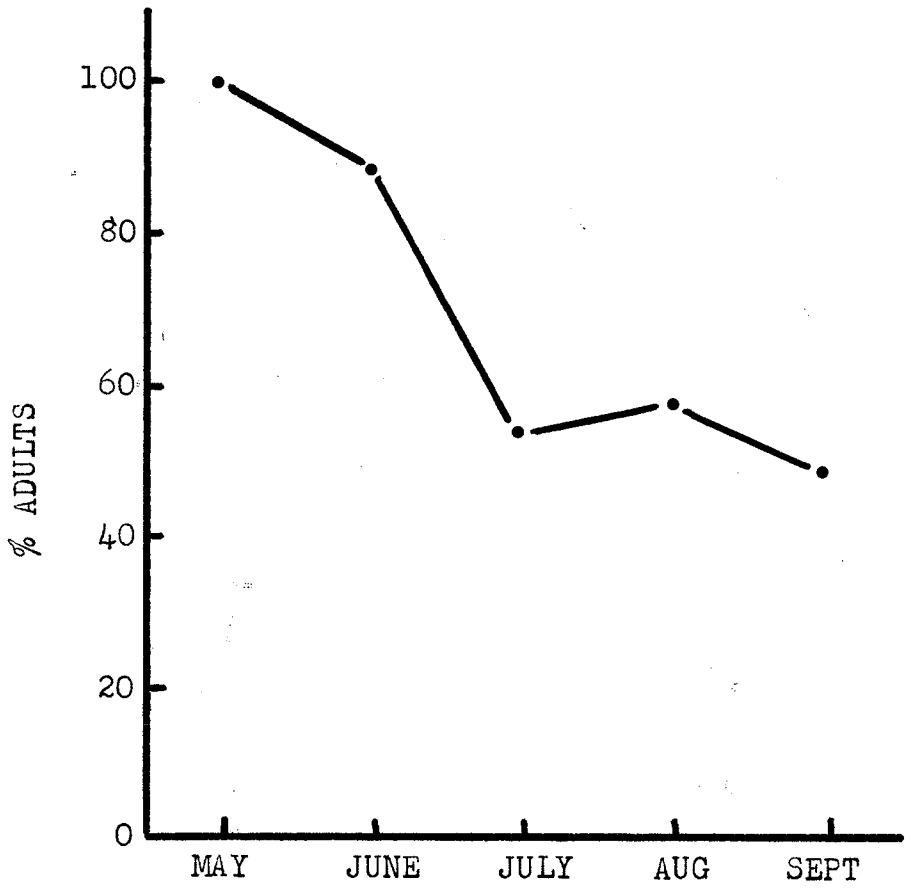


Figure 15.

Figure 16. Seasonal variation in incidence in Andrya macrocephala infections in voles in Michigan after Rausch and Tiner, 1949.

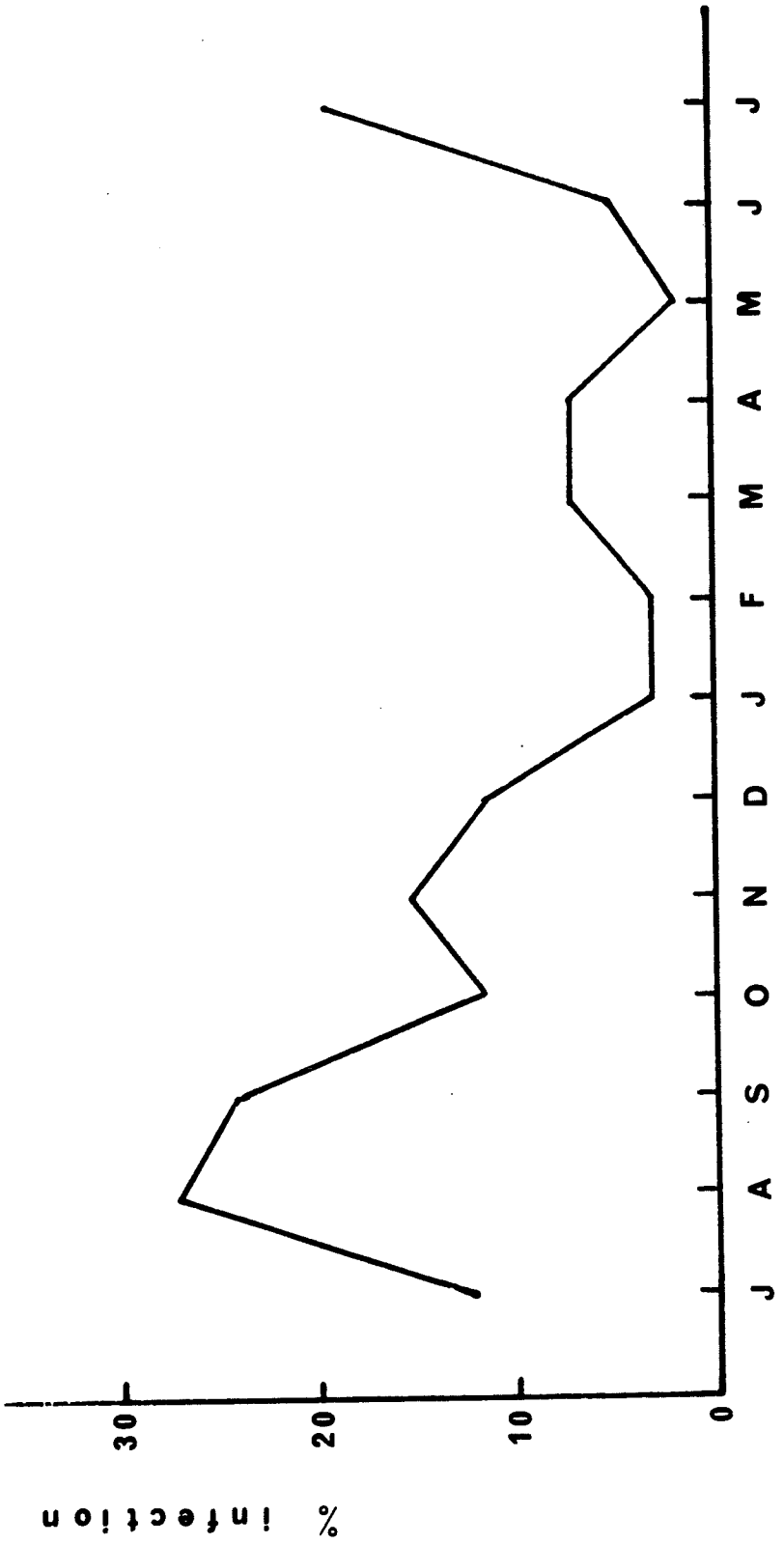


Figure 16.

Figure 17. Seasonal variation in incidence in *Andrya macrocephala* infections in voles in Manitoba.

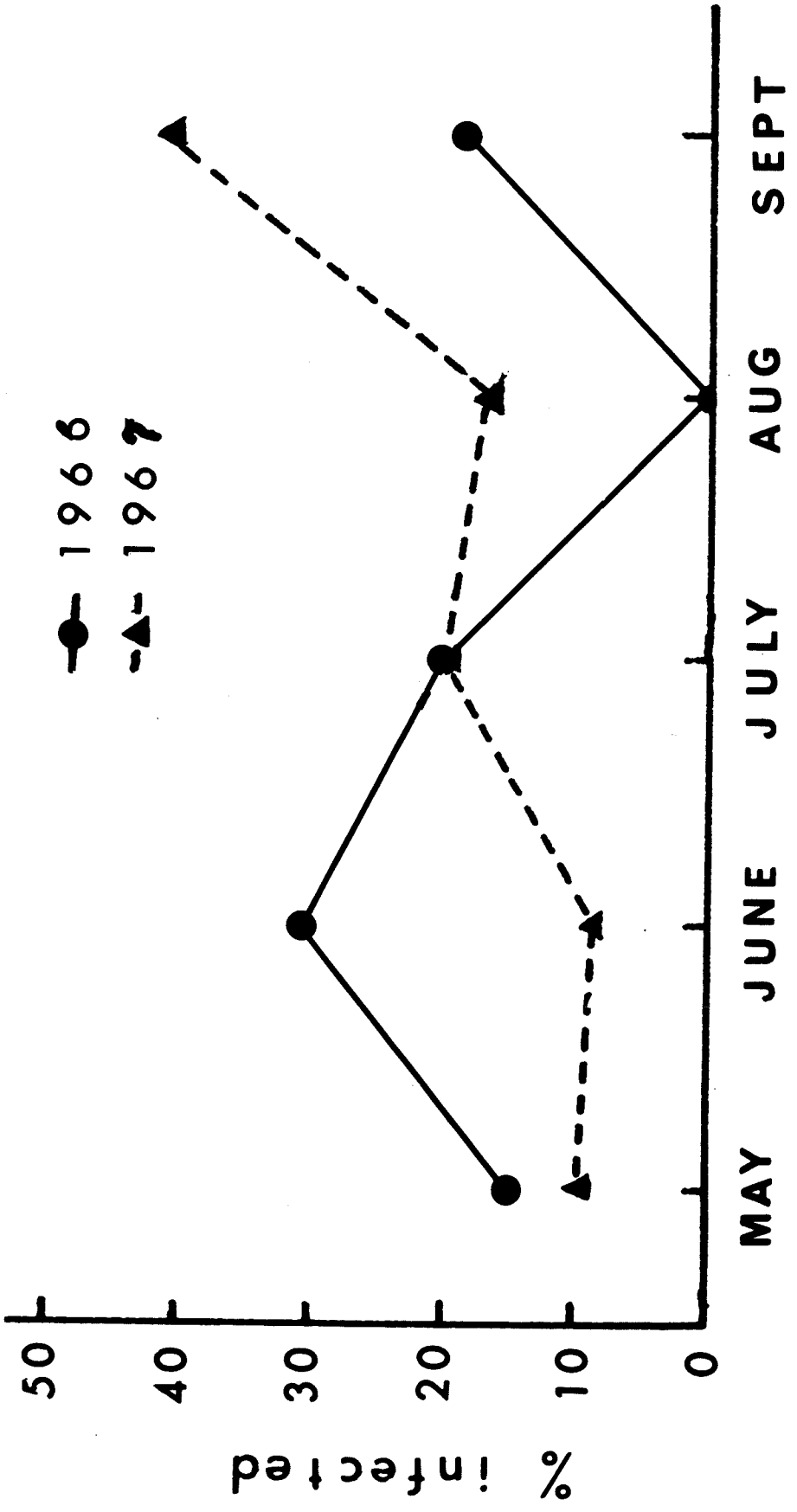


Figure 17.

well studied in North America. Rausch and Tiner (85) in 1949 conducted a survey of Microtus sp. in the North Central United States. They chose a 23 acre field in Michigan for extensive study. Three hundred and forty-five voles were removed at a uniform rate for thirteen months. If we compare Rausch and Tiner's curve for Andrya macrocephala (Fig.16) to ours (Fig.17), we see that they are similar. Their results and mine for 1967 show increases in incidence from May to July. My 1966 results are slightly different in that no helminths were found in August, though 67 voles were examined.

The above three curves show marked similarity in the period August to September. Differences between my results and those of Rausch and Tiner can probably be attributed to differing age composition of the rodent population.

Freeman and Wright (35) studied seasonal variations in the occurrence of Capillaria hepatica in rodents in Algonquin Park, Ontario, in 1956 (Table III, p.372). Although their samples were taken from several areas and were small, the authors stated that " if age structure of the Peromyscus maniculatus population is ignored, there is a pronounced decline in incidence from May through September". Such a decline was observed also in Manitoba (Fig.18). It ended in August, however, and was followed by a sharp rise in incidence in September.

Harkema (45) studied seasonal variation in the parasite

Figure 18. Seasonal variation in incidence in Capillaria hepatica infections in rodents from Delta (Area II) in 1967.

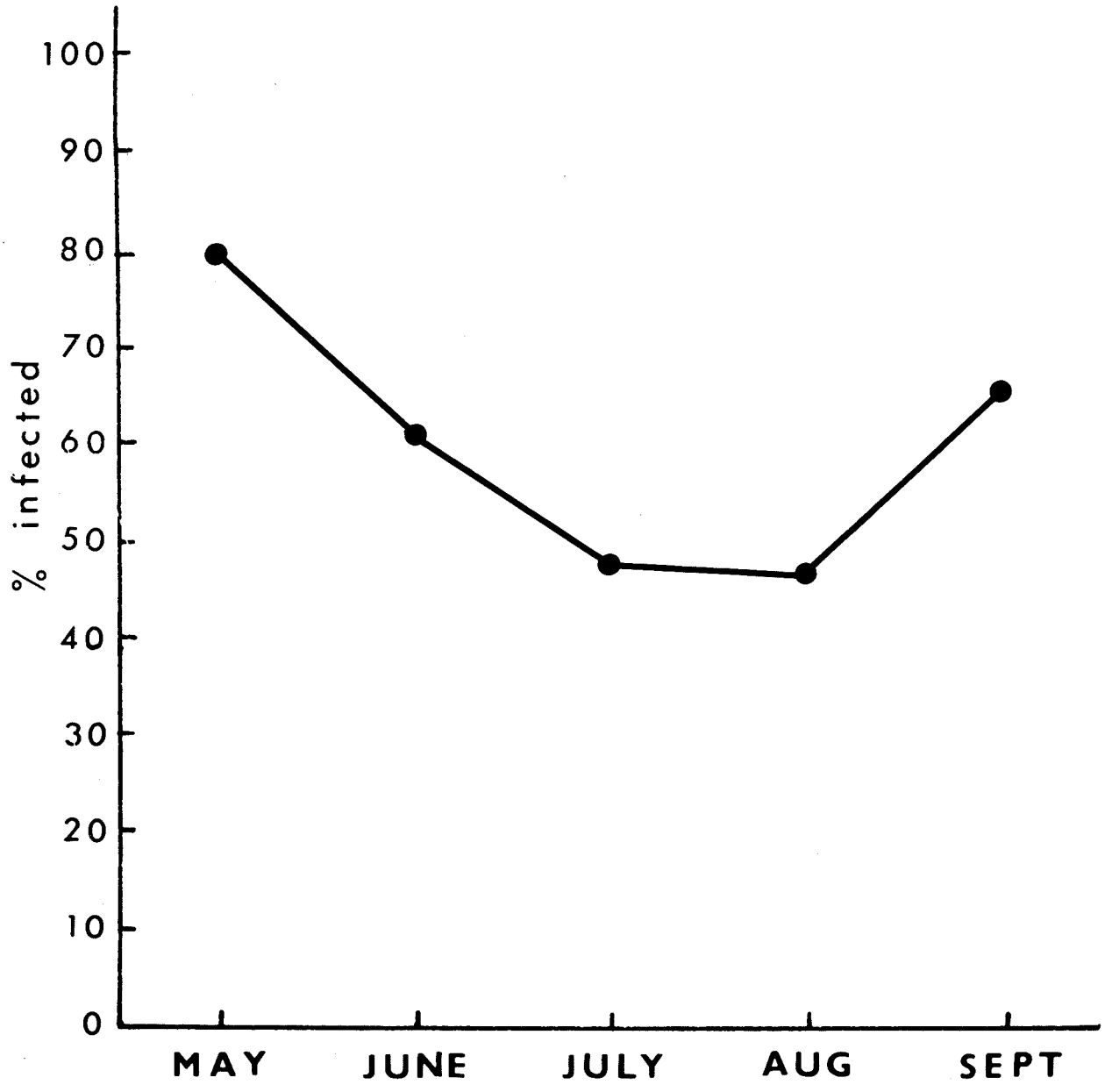


Figure 18.

Figure 19. Seasonal variations in incidence in Taenia mustelae infections in Microtus and Clethrionomys in 1966 and 1967.

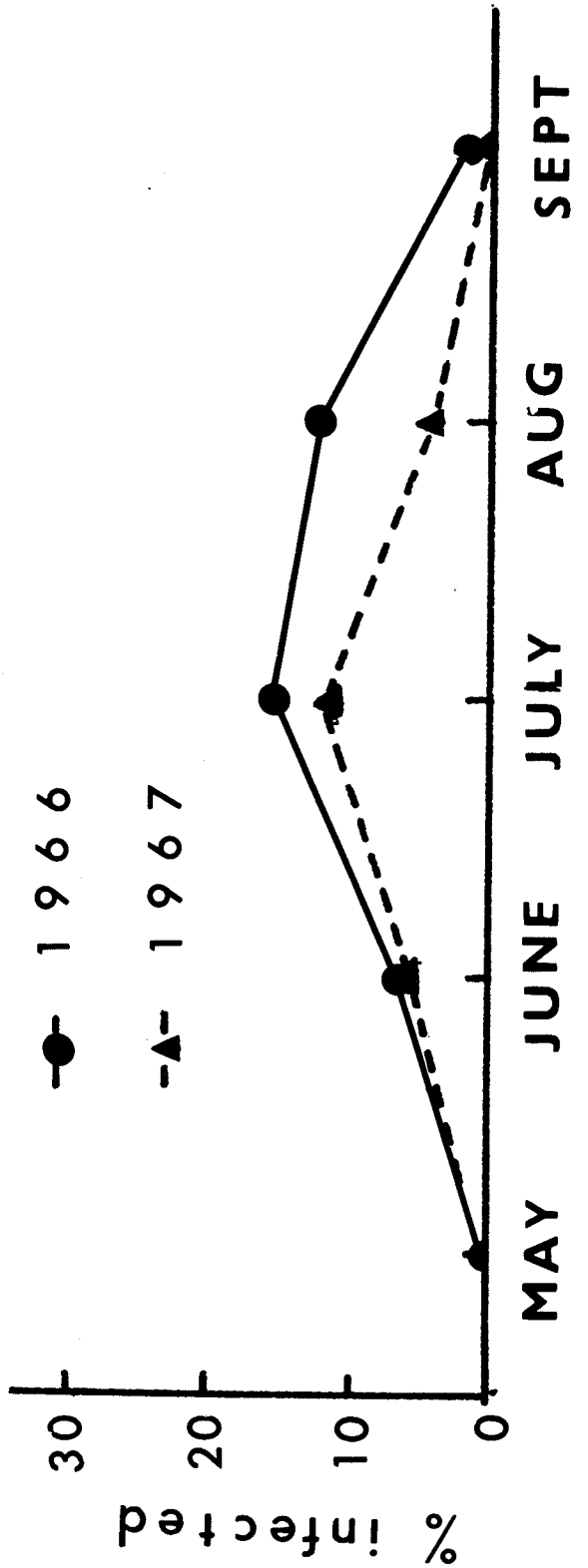


Figure 19.

fauna of rabbits (Sylvilagus floridanus mallurus) from October, 1933 to August, 1934. He observed peaks in April or May for Cittotaenia pectinata, Trichostrongylus affinis, and T. calcaratus. "No seasonal variation for Hasstilesia tricolor, Hymenolepis dimimuta, larval tapeworms, Trichosomoides crassicauda and Heterakis spumosa was demonstrated."

Boughton (10), in 1932, reported that in Western Canada, snowshoe rabbits develop an almost complete resistance to Cittotaenia with a change in diet in late July and August to fruit and berries. As was pointed out in the section dealing with Capillaria hepatica, Pavlov concluded that infections with this nematode were correlated to some extent with the diet.

Seasonal variations in incidence of infection with Taenia mustelae (Fig. 19) were not found.

It may be concluded that seasonal changes in helminth infections are due to: age composition of the rodent populations, sources of infection, and probably changes in diet.

Multiple species parasitism: In this survey, several instances of multiple species parasitism were found (Table IX). A maximum of four helminth species was present in one host.

Pavlovski (22) applied the term parasitocoenosis to the entire parasite population of one host. Dogiel (22) stated: "that the entire quantitative and qualitative composition of the parasite population of various hosts is determined

TABLE IX

Instances of Multiple Species Parasitism.

Host	Number of Species of Parasites					
	0	1	2	3	4	Total
Clethrionomys gapperi	145	104	27	1	1	278
Microtus pennsylvanicus	553	144	19	7	1	724
Peromyscus maniculatus	45	3				48
Totals:	743	251	46	8	2	1050

not only by the ecological factors and conditions which the host, as the micro-environmemt, has to offer, but also by the character of the interrelations between the individual species included in the parasitocoenosis. These interrelations are in some instances antagonistic, the presence of some species preventing the occurrence of members of another. When the relationship is of a synergistic character, one parasite increases the chances of the existence of thr other."

To test for these two effects among the helminths of Manitoba rodents, the observed cases of infection with two species of helminths were compared statistically with the expected number of cases. Only in the Andrya macrocephala - Capillaria hepatica parasitocoenosis was a significant difference found between the expected and observed infections. This positive correlation can only suggest the presence of synergism: the high infection rate with Capillaria hepatica in one biotope will influence the results of a statistical test, as it is so much higher than that of Andrya macrocephala (approximately 3 times as great for Clethrionomys gapperi, the dominant rodent in the lake-shore forest).

Synergism and antagonism can be studied only experimentally (22). Positive and negative correlations in the occurrence of parasite pairs may depend upon such factors as the use of the same intermediate hosts, habits of the definitive or intermediate hosts, and local envir-

mental influences on eggs and larvae.

Rodent parasites as human pathogens: Of the parasites found in this survey, only Capillaria hepatica is a potential human parasite. According to Calle (16), genuine and spurious human infection with this parasite should be carefully distinguished. In genuine infection the parasites are present in the liver where they deposit their ova. Clinical manifestations of infection develop, but the ova are not passed in the faeces. In spurious infection, the ova are simply passing through the digestive tract following the ingestion of an infected liver. In the Chagres River region of Panama, nine cases of such spurious infections with C. hepatica were found among 440 persons examined (31). Another report from the same region (32) mentions 16 spurious infections among the 194 persons examined. Two cases of spurious infection were described by McQuown (72) in Louisiana, in patients who ate gravy made from squirrel livers.

Genuine human cases of hepatic capillariasis are listed in Table X. Of the eight cases, six were diagnosed at necropsy, and the remaining two (those from South Africa and North Carolina) by biopsy. One survivor was treated with dithiazanine iodide (Delvex), and the other received no therapy.

The absence in southern Manitoba rodents of Echinococcus multilocularis which uses rodents as intermediate hosts and which is highly pathogenic to man, is noteworthy.

TABLE X

Cases of Human Infection with Capillaria hepatica

DATE	LOCALITY	AUTHOR AND REFERENCE
1924	India	MacArthur (66)
1950	Louisiana, U.S.A.	McQuown (72)
1954	Maryland, U.S.A.	Otto et al (74)
1954	Turkey	Turhan et al (104)
1956	Hawaii	Ewing et al (30)
1957	Johannesburg, S. Africa	Cochrane et al (19)
1959	Louisiana, U.S.A.	Ward et al (107)
1961	North Carolina, U.S.A.	Calle (16)

This cestode was reported in 1952 by Rausch (80) from Microtus oeconomus from St. Lawrence Island in the Bering Sea; by Rausch (81) from Arctic foxes from Resolute Bay, Cornwallis Island; by Choquette et al (18) from Eskimo Point, North West Territories; in 1964 by Leiby and Olsen (60) in Red foxes in North Dakota; by Leiby (59) in 1965 in Microtus pennsylvanicus and Peromyscus maniculatus, also in North Dakota. Recently, Hnatiuk (46) found it in an M. pennsylvanicus in Saskatchewan. One would expect, therefore, to find E. multilocularis in Manitoba rodents. Despite the examination of 1061 rodent livers from southern Manitoba, I was unable to find it.

CONCLUSIONS

1) Eleven species of helminths (seven of cestodes and four of hematodes) were found in three species of Manitoba rodents.

2) Ten specimens of Zapus hudsonius examined were free of helminths.

3) The findings of Andrya bairdi, Capillaria hepatica, and Heligmosomum costellatum in Microtus pennsylvanicus drummondi represent new host records.

4) The findings of Andrya bairdi and Heligmosomum microti in Clethrionomys gapperi loringi represent new host records.

5) The helminthofauna of rodents from different biotopes varies both in the number of species present and in the incidnece of infection. The disturbed grassland and lakeshore forest areas had seven species of helminths each, while the other areas had three each. Andrya macrocephala and Taenia mustelae were the only parasites common to all five biotopes.

6) Focal distributions of cestodes are probably due to the presence, or absence, of the other hosts involved in the parasite life cycles. Foci of nematodes, however, are most likely influenced by the climatic conditions of the various biotopes; dampness was found to strongly influence the presence of nematodes.

7) A focus of Capillaria hepatica was found in the Delta lakeshore forest, where 47.5% of Clethrionomys gapperi loringi were infected.

8) Seasonal variation in the percent infection of rodents was studied in 1966 and 1967. This variation was attributed to age composition of the rodent population and their feeding habits.

9) No statistical evidence of correlative occurrence of members of the parasite pairs was found.

10) The only rodent parasite found that may be pathogenic to humans was Capillaria hepatica.

APPENDIX I

On June 30, 1968 I examined 98 *Peromyscus maniculatus bairdi* from gravel pits near Stonewall, Manitoba. In seven of them, *Catenotaenia dendritica* (Goeze, 1782) was found in the small intestine. The finding of this cestode in *P. m. bairdi* is a new host record, and only the second finding of this parasite in *Peromyscus* in North America.

APPENDIX II

Parasitism of Voles by Cuterebra sp. (Diptera: Cuterebridae)

During the course of the helminthological survey, parasitism of voles with larvae of Cuterebra (Myiasis) was noted.

Three previous instances of Cuterebra myiasis were recorded in Manitoba. In 1940, Allen (2) recorded a case of myiasis in a house mouse. McLeod (73) also found infections in a house mouse and a mink; and Buchner (13), in 1958, observed myiasis in Microtus pennsylvanicus drummondi, Clethrionomys gapperi loringi, and Peromyscus maniculatus bairdi. Other records of Cuterebra parasitism are summarized in Table XI.

Life cycle: The Cuterebridae are known only from North and South America and usually have a single generation per year that is well synchronized with the activity of their hosts. Adult Cuterebra hatch from puparia in June or July. They oviposit near the shelter or over-winter sites of the host. Larvae hatch from the eggs and somehow reach their host while in the early first instar. They enter the host through the skin and burrow into the subcutaneous tissues. They remain near the site of initial penetration or wander elsewhere. A hole appears at the resting site for respiration and waste removal. As the larva develops through the second and third instars, it increases

in bulk, reaching a weight of one gram or more. After a maturation period of approximately twenty-eight days, the larva emerges from its host, burrows into the soil, and soon pupates. It overwinters in this stage and emerges as the adult fly in next June or July.

Results: Sixty voles out of a total of 1061 were infected with Cuterebra: fifty-six Microtus pennsylvanicus, three Clethrionomys gapperi, and one Peromyscus maniculatus.

Eighty-one larvae were found in Microtus pennsylvanicus, with a mean of 1.45 per infected animal. This figure falls within the 1.0 to 1.8 range recorded by Wecker (109) in 1962, and close to the 1.6 larvae per host as recorded by Sillman (95) in 1955. The highest number of larvae per individual was five, and the lowest,one; this is not the highest recorded, as Sillman (95) found one Peromyscus with seven bots.

I found that 36 (60%) of the infected rodents were males and 24 (40%) were females. Goertz (37) recorded similar percentages: 62% males and 38% females. Sealander's (93) findings also showed a higher infection for males, but Sillman (95) reported the opposite for Cuterebra angustifrons in white-footed mice. Wecker (109) found no correlation with sex.

In 1966, the first infection with Cuterebra was observed on July 22; in 1967, on July 26. Peaks in infection were found in the first week of August in 1966, and

the third week of August in 1967. This coincides with the work of several authors (37, 93, 95, 102, 109). Other workers (1, 20, 91) observed peaks from September to October, but their work was done in a more southern latitude. The later peaks probably reflect a climatic difference and may be related to the larval diapause discovered by Sillman (96).

Of the infections, only two were observed to be scrotal, all others being located at the anterior end of the body. The larvae were all arranged nearly parallel to the longitudinal axis of the host, as noted by Sillman (95). Secondary abscesses were also noted in a number of cases, and may be due to "in situ" death of the larvae or an immunological reaction by the host. The wounds were surrounded by a large area of thick connective tissue.

Discussion: The infections of voles with Cuterebra are probably due to C. grisea, though the larvae were not identified to species. Buchner (13) stated that "this species is the only member of the family that has been collected in the Prairie Provinces, so that it is likely that all the following records of cuterebrids pertain to the species C. grisea".

TABLE XI

Infections with *Cuterebra* in voles in North America, during periods of peak abundance.

AUTHOR	HOST	INFECTION	LOCALITY
Scott and Snead (91)	*Peromyscus*	30-35%	Iowa
Dalmat (20)	"	38%	Iowa
Test and Test (102)	"	29%	Indiana
Sillman (95)	"	28%	Ontario
Wecker (109)	"	48%	Michigan
Abbott and Parsons (1)	"	27%	Massachusetts
Sealander (93)	"	32%	Ontario
Goertz (37)	"	7-18%	Oklahoma
Goertz (loccit)	*Neotoma*	27%	Oklahoma

References

1. Abbott, H. G. and Parsons, M.A. 1961. Cuterebra infestations in Peromyscus. J. Mammal. 42: 383-385.
2. Allen, J. A. 1940. Principles of Mink Ranching, Game and Fisheries Branch, Manitoba.
3. Ameel, D. J. 1942. Two larval cestodes from the muskrat. Trans. Am. Microsc. Soc. 61: 267-271.
4. Baer, J. G. 1927. Monographie des cestodes de la famille des Anoplocephalidae. Bull. Bio. France et Belgique, suppl. 10: 1-241.
5. Baer, J. G. 1932. Contribution a la faune helminthologique de Suisse. (Deuxieme partie). Rev. suisse zool. 39: 1-57.
6. Bailey, V. 1926. A biological survey of North Dakota. N. Amer. Fauna. 49. U.S. Dept. Agric.
7. Barker, F. D. 1915. Parasites of the American muskrat (Fiber zibethicus). J. Parasitol. 1: 184-197.
8. Baylis, F. D. 1931. On the structure and relationships of the nematode Capillaria (Hepaticola) hepatica (Bancroft). Parasitology, 23: 533-543.
9. Borrel, A. 1906. Cancers et helminthes. Bull. Acad. Med. 55: 591.
10. Boughton, R. 1932. The influence of helminth parasitism on the abundance of the snowshoe rabbit in Western Canada. Can. J. Res. 7: 524-547.

11. Buchner, C. H. 1955. A simple permanent livetrap plot for shrews. J. Mammal. 36: 286.

12. Buchner, C. H. 1957. Population studies on small mammals of southeastern Manitoba. J. Mammal. 38: 87-97.

13. Buchner, C. H. 1958. Cuterebrids (Cuterebra grisea Coq.) attacking small mammals. Bi-monthly Progress Report, Can. Dept. Agric. Sci. Service - Forest Biol. Division, 14: 2-3.

14. Bullock, F. D. and Curtis, M. R. 1920. The experimental production of sarcoma of the liver of rats. Proc. N. Y. Path. Soc. 20: 149-175.

15. Bullock, F. D. and Curtis, M. R. 1928. A cysticercus carcino-osteochondrosarcoma of the rat liver with miltiple cysticercus sarcoma. J. Cancer Res. 12: 326-334.

16. Calle, S. 1961. Parasitism by Capillaria hepatica. Pediatrics, 27: 648-655.

17. Cameron, T. W. M. and Parnell, I. W. 1933. The internal parasites of land mammals in Scotland. Proc. Roy. Phys. Soc. Edinburgh, 22: 133-154.

18. Choquette, L. P. E., MacPherson, A. H., and Cousineau, J. G. 1962. Note on the occurrence of Echinococcus multilocularis Leuckart, 1863, in the Arctic fox in Canada. Can. J. Zool. 40: 1167.

19. Cochrane, J. C. , Sagorin, L., and Wilcocks, M.G. 1957. Capillaria hepatica infection in man. S. Afr. Med. J. 31: 751.

20. Dalmat, H. T. 1942. A new parasitic fly (Cuterebridae) from the northern white-footed mouse. J. N.Y. Ent. Soc. 50: 45-52.

21. Dobrovsky, C. G. and Harbough, M. J. 1934. Cysticercus fasciolaris from the red squirrel. Trans. Am. Microsc. Soc. 53: 67.

22. Dogiel, V.A. 1964. General parasitology. Oliver and Boyd Ltd. London.

23. Douthitt, H. 1915. Studies on the cestode family Anoplocephalidae. Illinois Biol. Monogr. 1: 355-446.

24. Dunagan, T. T. 1957. Helminth parasites of Alaska muskrats. Trans. Am.Microsc. Soc. 76: 318-320.

25. Dunning, W. F. and Curtis, M. R. 1946. Multiple peritoneal sarcoma in rats from intraperitoneal injection of mashed, ground Taenia larvae. Cancer Res. 6: 668-670.

26. Edwards, R. L. 1949. Internal parasites of Central New York muskrats (Ondatra zibethica L.), J. Parasitol. 35: 547-548.

27. Elton, C., Ford, E., and Baker, I. 1931. The health and parasites of a wild mouse population. Proc. Zool. Soc. London, 1931, 657-721.

28. Erhardova, B. 1955. Die Helminthofauna der mäuse-artigen Nagetiere des Nationalparks in der hohen Tatra. Zool. a entomol. listy, 4: 353-364.

29. Erickson, A. B. 1938. Parasites of some Minnesota Cricetidae and Zapodiadae, and a host catalogue of helminth parasites of native American mice. Am. Midland Naturalist, 20: 575-589.

30. Ewing, G. M. and Tilden, I. L. 1956. Capillaria hepatica: report of fourth case of true human infestation. J. Pediat. 48: 341.

31. Faust, E. C. 1931. Investigations in Panama during the summer of 1930. Science, 73: 43.

32. Faust, E. C. and Marinex, W. H. 1935. Notes on helminths from Panama. II. Rare human nematode eggs in the faeces of individuals from the Chagres River, Panama. J. Parasitol.21: 332.

33. Firlotte, W. A. 1948. A survey of the parasites of the brown Norway rat. Can. J. Comp. Med. 12: 187-191.

34. Freeman, R.S. 1956. Life history studies on Taenia mustelae, Gmelin, 1790 and the taxonomy of certain taeniid cestodes from Mustelidae. Can. J. Zool. 34: 219-242.

35. Freeman, R. S. and Wright, K.A. 1960. Factors concerned with the epizootiology of Capillaria hepatica (Bancroft, 1893) (Nematoda) in a

population of Peromyscus maniculatus in Algonquin Park, Canada. J. Parasitol.46: 373-382.

36. Gmelin, J. F. 1790. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus differentiis, sunonymis, locis. Vol. 1. Pt. 6 (Vermes). Lipsiae.

37. Goertz, J. W. 1966. Incidence of warbles in some Oklahoma rodents. Am. Midland Naturalist, 75: 242-245.

38. Goeze, J. A. E. 1782. Versuch einer Natugeschichte der Eingeweidewürmer thierischer Körper. Blankenburg.

39. Grundmann, A.W. and Frandsen, J.C. 1960. Definitive host relationships of the helminth parasites of the deer mouse, Peromyscus maniculatus, in the Bonneville Basin of Utah. J. Parasitol. 46: 673-677.

40. Gunderson, H. L. and Beer, J. H. 1953. The mammals of Minnesota. Univ. of Minnesota Press.

41. Hall, M.C. 1916. Nematode parasites of mammals of the orders Rodentia, Lagomorpha, and Hyracoidea. Proc. U.S. Nat. Mus. 50: 1-258.

42. Hall, M. C. 1919. The adult taenioid cestodes of dogs and cats and of related carnivores in North America. Proc. U.S. Nat. Mus. 55: 1-94.

43. Hall, J. E. and Sonnenberg, B. 1955. Some helminth parasites of rodents from localities in Mary-

land and Kentucky. J. Parasitol. 41: 640-641.

44. Hansen, M. F. 1947. Three anoplocephalid cestodes from the prairie meadow vole, with description of Andrya microti n. sp. Trans. Am. Microsc. Soc. 66: 279-282.

45. Harkema, R. 1936. The parasites of some N. Carolina rodents. Ecol. Monogr. 6: 151-232.

46. Hnatiuk, J. M. 1966. First occurrence of Echinococcus multilocularis Leuckart, 1863 in Microtus pennsylvanicus in Saskatchewan. Can. J. Zool. 44: 493.

47. Hughes, R. C. 1941. The taeniae of yesterday. Bull. Okla. Agric. Mech. Coll. 38: 1-83.

48. Joyeux, C. E. and Baer, J. G. 1934. Sur quelques cestodes de France. Arch. Muséum nat. hist. nat. 6 sér. 11: 157-171.

49. Joyeux, C. H. and Baer, J. G. 1945. Morphologie, évolution et position systématique de Catenotaenia pusilla (Goeze, 1782), cestode parasite de Rongeurs. Rev. suisse Zool. 52: 13-51.

50. Joyeux, C. E. and Baer, J. G. 1936. Cestodes. Faune de France, Fed. franc. soc. sci. nat. 30: 1-613.

51. Kinsella, J. M. 1967. Helminths of Microtinae in Western Montana. Can. J. Zool. 45: 269-274.

52. Kirschenblatt,J. D. 1938. Die Gesetzmässigkeiten der Dynamik der Parasitenfauna bei den mauseähnlichen Nagetieren (Muriden) in Transkaukasien. Diss. Univ. Leningrad, pp. 5-92.

53. Knight, J. M. 1951. Diseases and parasites of the muskrat (Ondatra zibethica) in British Columbia. Can. J. Zool. 29: 188-214.

54. Küchenmeister, G. F. H. 1955. Die in und an dem Körper des lebenden Menschen vorkommenden Parasiten. Leipzig.

55. Küchenmeister, G. F. H. 1858. Ueber Leptus autom-nalis (Erntemilbe). Amtl. Ber. 32. Versamml. Deut. Naturf. u. Aerzte (1856). p.254.

56. Kuns, M. L. and Rausch, R. 1950. An ecological study of helminths of some Wyoming voles (Microtus spp.) with a description of a new species of Nematospiroides (Heligmosomidae: Nematoda). Zoologica, 35: 181-188.

57. Law, R. G. and Kennedy, A. H. 1932. Parasites of fur-bearing animals. Bull. (4) Ontario Dept. Game and Fish, 30 pp.

58. Leiby, P. D. 1962. Helminth parasites recovered from some rodents in Southeastern Idaho. Am. Midland Naturalist, 67: 250.

59. Leiby, P. D. 1965. Cestode in North Dakota: Echinococcus in field mice. Science, 159: 763.

60. Leiby, P. D. and Olsen, O. W. 1964. The cestode Echinococcus multilocularis in foxes in North Dakota. Science, 145: 1066.

61. Leuckart, K. G. F. R. 1856. Die Blasenbandwürmer und ihre Entwicklung. Zugleich ein Beitrag zur Kenntiss der Cysticercus - Leber. Giessen.

62. Levin, M. _____. Small mammals and vegetation in the Lake Manitoba shore forest. (Unpublished manuscript).

63. Locker, B. 1955. The identification of Taenia tenuicollis Rudolphi, 1819, in North America. J. Parasitol. 41: 51-56.

64. Lubinsky, G. 1956. On the probable presence of parasitic liver cirrhosis in Canada. Can. J. Comp. Med. 20: 457-465.

65. Lubinsky, G. 1957. List of helminths from Alberta rodents. Can. J. Zool. 35: 623-627.

66. MacArthur, W. P. 1924. A case of infestation of human liver with Hepaticola hepatica (Bancroft, 1893) Hall, 1916: with sections from the liver. (Section of Tropical Diseases and Parasitology) Proc. Roy. Soc.Med. 17: 83-84.

67. Martin, H. M. 1930. Notes on cestode larvae. J. Am. Vet. Med. Assoc. 29: 804-805; 807-810.

68. McCoy, G. W. 1909. Pathological conditions found in rats. P. H. Rept's, U.S. Pub. Health and Mar. Hosp. Serv. Bull. Hyg. Lab. 23: 1365-1371.

69. McIntosh, A. 1941. A new dilepid cestode Catenotaenia linsdalei, from a pocket gopher in California. Proc. Helminthol. Soc. Wash. 8: 60-62.

70. McLeod, J. A. 1933. A parasitological survey of the genus Citellus in Manitoba. Can. J. Res. 9: 108-127.

71. McQuown, A. L. 1950. Capillaria hepatica; report of genuine and spurious cases. Am. J. Trop. Med. 30: 761-767.

72. McQuown, A. L. 1950. Capillaria hepatica. Am. J. Clin. Path. 24: 448.

73. Murray, V. I. E. 1965. A study of myiasis in man and other animals in Manitoba. Master's thesis. University of Manitoba.

74. Otto, G. F., Berthrong, M., Abbleby, R. E. , Rawlins, J. C., and Wilbur, O. 1954. Eosinophilia and hepatomegaly due to Capillaria hepatica infection. Bull. Johns Hopkins Hosp. 94: 319-336.

75. Peterson, L. R. 1966. The mammals of eastern Canada. Oxford Univ. Press.

76. Rausch, R. 1946. Paranoplocephala troeschi, new species of cestode from the meadow vole, Microtus p. pennsylvanicus Ord. Trans. Am.

Microsc. Soc. 65: 354-356.

77. Rausch, R. 1948. Notes on cestodes of the genus Andrya Railliet, 1883, with the description of A. ondatrae n. sp. (Cestoda: Anoplocephalidae). Trans. Am. Microsc. Soc. 67: 187-191.

78. Rausch, R. 1950. Observations on a cyclic decline of lemmings (Lemmus) on the Arctic Coast of Alaska during the spring of 1949. Arctic 3: 166-177.

79. Rausch, R. 1951. Studies on the helminth fauna of Alaska. VIII. - On some helminths from Arctic marmots with the description of Catenotaenia reggiae n. sp. (Cestoda - Anoplocephalidae). J. Parasitol. 37: 415-417.

80. Rausch, R. 1952. Studies on the helminth fauna of Alaska. XI. Helminth parasites of microtine rodents - taxonomic considerations. J. Parasitol. 38: 415-444.

81. Rausch, R. 1956. Studies on the helminth fauna of Alaska. XXX. The occurrence of Echinococcus multilocularis Leuckart, 1863, on the mainland of Alaska. Am. J. Trop. Med. Hyg. 5: 1086-1092.

82. Rausch, R. 1957. Distribution and specificity of helminths in microtine rodents: evolutionary implications. Evol. 11: 361-368.

83. Rausch, R. and Schiller, E. L. 1949. Some observations on cestodes of the genus Paranoplocephala Luehe, parasitic in North American voles (Microtus spp.). Proc. Helminthol. Soc. Wash. 16: 23-31.

84. Rausch, R. and Schiller, E. L. 1949. A critical study of North American cestodes of the genus Andrya with special reference to A. macrocephala Douthitt, 1915. (Cestoda: Anoplocephalidae). J. Parasitol. 35: 306-314.

85. Rausch, R. and Tiner, J. D. 1949. Studies on the parasitic helminths of the North Central States. II. Helminths of voles (Microtus spp.). Preliminary report. Am. Midland Naturalist, 41: 665-694.

86. Read, C.P. and Millemann, R. E. 1953. Helminth parasites in Kangaroo rats. Univ. Calif. Publications in Zool. 59: 61-80.

87. Rudolphi, C. A. 1810. Entozoorum sive vermium intestinalium historia naturalis. Vol. II. Amstelaedami.

88. Rudolphi, C. A. 1819. Entozoorum synopsis cui accedunt mantissa duplex et indices locupletissimi. Berolini.

89. Schad, G. A. 1954. Helminth parasites of mice in Northeastern Quebec and the coast of Labrador. Can. J. Zool. 32: 215-224.

90. Schad, G. A. 1956. Helminths recovered from deer mice Peromyscus maniculatus trapped in the Morgan Arboretum, Macdonald College, Province of Quebec. Can. J. Zool. 34: 208.

91. Scott, T. G. and Snead, E. 1942. Warbles in Peromyscus leucopus noveboracensis. J. Mammal. 23: 94-95.

92. Scoggan, H. J. 1957. The flora of Manitoba. Nat. Mus. Can. Bull. 140.

93. Sealander, J. A. 1961. Haematological values in deer mice in relation to botfly infection. J. Mammal. 42: 57-60.

94. Sillman, E. I. 1953. Microtus p. pennsylvanicus, a new final host for Opisthorchis tonkae Wallace and Penner, 1939 (Trematoda: Opisthorchidae). J. Parasitol. 35: 22.

95. Sillman, E. I. 1953. Studies on the biology of a cuterebrid (Cuterebridae: Diptera) infesting Peromyscus leucopus noveboracensis, Fischer, the White-footed mouse, in Southern Ontario. Ann. Rept. Ent. Soc. Ont. 86: 89-97.

96. Sillman, E. I. 1956. Further laboratory and field observations on the ecology of some Ontario Cuterebridae (Diptera), in particular, Cuterebra angustifrons Dalmat, 1942. Ann. Rept. Ent. Soc. Ont. 87: 28-40.

97. Skinker, M. S. 1935. A redescription of Taenia tenuicollis Rudolphi, 1819, and its larva, Cysticercus talpae Rudolphi, 1819. Parasitology, 27: 175-185.

98. Skrjabin, K. E., Shikhobalova, N.P., and Shul'ts, R. E. D. 1954. Dictyocaulidae, Heligmosomatidae, and Ollulanidae of animals. Russian text. Osnovy nematodologii. Vol. 4. Moscow.

99. Soltys, A. 1949. Parazyty wewnetrzne drobnych gryzoni lesnych (Muridae) Parku Narodowego w Bialowiezy. Ann. Univ. Mariae Curie-Sklodowska, 4: 233-259.

100. Tenora, F. 1958. Beitrag zur Helminthofauna der kleinen Erdsäugetiere des Altvatergebirges. Prir. sbor. Ostra. kraje, 19: 343-459.

101. Tenora, F. 1967. The helminthofauna of small rodents of the Rohacska Dolina Valley (Liptovske Hole Mts., Slovakia). Acta. sc. nat. Brno. 1: 29-68.

102. Test, F. H. and Test, A. R. 1943. Incidence of dipteran parasitosis in populations of small mammals. J. Mammal. 24: 506-508.

103. Thienemann, J. W. 1906. Untersuchungen über Taenia tenuicollis Rud. mit Berücksichtigung der übrigen Musteliden-Taenien. Arch. Naturgeschichte, 1: 227-248.

104. Turhan, B. 1954. Insan karasigerinde: Capillaria hepatica (Bancroft, 1893), Travassos, 1915. Mikrbiol. Dergisi, 7: 149.

105. Voge, M. 1948. New rodent hosts for Catenotaenia linsdalei, with an additional description of this cestode. Trans. Am. Micros. Soc. 67: 266-267.

106. Walker, J. M. 1959. Vegetation studies on the Delta Marsh, Delta, Manitoba. Master's thesis, University of Manitoba.

107. Ward, R. L., and Dent, H. H. 1959. Capillaria hepatica infection in a child. Bull. Tulane Med. Fac. 19: 27.

108. Wardle, R. A., and McLeod, J. A. 1952. The Zoology of Tapeworms. Univ. of Minnesota Press, St. Paul.

109. Wecker, S. C. 1962. The effects of bot fly parasitism on a local population of white footed mouse. Ecol. 43: 561-565.

110. Wright, H. E. 1938. Further observation on the incidence of Hepaticola (Capillaria) hepatica ova in human faeces. Am. J. Trop. Med. 18: 329-330.

111. Yamaguti, S. 1942. Studies on the helminth fauna of Japan. Part 42. Cestodes of mammals II. Kyoto, Japan.

112. Yorke and Maplestone. 1926. The Nematode Parasites of Vertebrates. J. and A. Churchill, London.

113. Zeder, J. G. H. 1803. Anleitung zur Naturgeschichte der Eingeweidewürmer. Bamberg.