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Author(s)	ISHIMOTO, Yasuo
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STUDIES ON HELMINTHS OF VOLES IN HOKKAIDO
II ECOLOGICAL STUDY

Yasuo ISHIMOTO
Department of Parasitology
Faculty of Veterinary Medicine
Hokkaido University, Sapporo, Japan

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Setting aside the host specificity, the food habit is the most important of the various ecological factors concerning voles. The herbivorous vole has less chance of being infected with cestodes than the insectivorous vole. No sex resistance of voles to helminth infections was revealed. The increase of incidence of helminths with the progress of host's age was observed in the cases of helminth species, *Paranoplocephala omphalodes, Coronacanthus apodemi, Heligmosomum yamagutii, Longistriata hokkaidensis, Mammaniduloides hokkaidensis* and *Capillaria hepatica*. This phenomenon can be explained by the increased chances of infection with the progress of the host's age. The seasonal analysis of helminth fauna was discussed, classifying the year into 5 periods. Younger animals play a main role in the abrupt reduction of the incidence of *H. yamagutii*. Older voles cause a higher increase in the incidence of *C. hepatica* and *M. hokkaidensis*. A high incidence of *C. apodemi* and *Plagiorchis muris* in the summer is attributable to the abundance of invertebrate intermediate hosts in this season. The increase of *Syphacia montana* in the autumn and spring originates in the increase of opportunities for contact of voles in the reproductive seasons. In two species, *C. apodemi* and *C. hepatica*, significant differences between the two experimental areas were proved about their incidences. The difference of arthropod fauna by area is suspected concerning these helminths, since they require arthropods as intermediate hosts or disseminators in their life cycles.

INTRODUCTION

In the preceding paper[5], the author clarified the helminth fauna of voles in Hokkaido; he described 15 species, including one new species, *Heligmosomum kobayashii*, and two of new distribution records, *Paranoplocephala omphalodes* and *Cladothyridium* sp.

In the present part, the author discusses the host-parasite relationship in connection with the ecology of host animals, since many problems are left for study.

MATERIALS AND METHODS

The voles examined were provided by members of the Hokkaido Group of

Field Mouse Research. As shown in the preceding papers, the voles were captured in three days of the first week of each month, from June 1967 to May 1968, at the Nopporo National Forest (43°25′N, 141°25′E) in the vicinity of Nopporo, 20 km east of Sapporo, Hokkaido. Two experimental areas 2 km apart were chosen; one was natural forest and the other was artificial forest. In each experimental area, 50 snap-traps were laid at intervals of 10 m on a straight line. The number of cases examined were 165 of *Clethrionomys rufocanus bedfordiae* (THOMAS), 183 of *Apodemus argenteus hokkaidi* (TEMMINCK et SCHLEGEL) and 67 of *A. speciosus ainu* (THOMAS) (tab. 1). Sex, weight and body-length were recorded at the time of capture.

The age of the animals was determined by the development of the molar, through applying the methods of ABE (1966, unpublished) for *C. rufocanus*, and FUJIMAKI (1966) and HIRAIWA (1958) for *A. argenteus* and *A. speciosus*.

A survey of the flora and invertebrate fauna of the experimental areas was conducted by the members of the research group above-noted. They also studied the ecology and population dynamics of voles. In this paper, with their permission, the author has adopted some of these data.

RESULTS AND DISCUSSION

A Differences among helminth fauna according to host species

Considerable differences among helminth fauna according to host species could be observed, although the three rodent species examined were captured in the same place. The difference might be explained partly by the host specificity; however, it may also be attributable to ecological differences in the hosts.

The distribution of the helminth species in the host animals is shown in tables 1 and 2. As shown in table 1, 3 helminths, *Heterakis spumosa*, *Mammaniduloides hokkaidensis* and *Plagiorchis muris*, were common to the all hosts. Adult cestodes, however, were limited to *Apodemus*. Generally speaking, *Clethrionomys rufocanus* and *Apodemus speciosus* are parasitized by 1 or 2 species of helminths, and *A. argenteus* by 2 or 3. General incidence was 86% in *C. rufocanus*, 97.3% in *A. argenteus* and 94.0% in *A. speciosus*. A difference in the infective rate of *Syphacia emileromani* was noted between *A. argenteus* and *A. speciosus*: 86.3% and 31.8%, respectively. *Heligmosomum yamagutii* and *Syphacia montana* in *C. rufocanus*, and *Longistriata hokkaidensis* and *Heligmosomum kobayashii* in the two *Apodemus* species indicated the host specificity.

Ecological differences of field mice in Hokkaido were studied by OTA (1968). He states that *C. rufocanus* is a herbivorous semi-fossorial animal, *A. argenteus* a carpo-insectivorous arboreal and *A. speciosus* a carpo-insectivorous terrestrial.

TABLE 1 *Number of hosts infected*

HELMINTHS	HOST SPECIES *Clethrionomys rufocanus* (165)*1	*Apodemus argenteus* (183)	*Apodemus speciosus* (67)
Nematoda			
Heligmosomum yamagutii CHABAUD, RAUSCH & DESSET, 1963	120	—	—
Heligmosomum kobayashii n. sp.*2	—	13	2
Mammaniduloides hokkaidensis OHBAYASHI, ORIHARA & FUJIMAKI, 1968	19	14	1
Longistriata hokkaidensis CHABAUD, RAUSCH & DESSET, 1963	—	174	63
Heterakis spumosa SCHNEIDER, 1866	20	3	1
Syphacia emileromani CHABAUD, RAUSCH & DESSET, 1963	—	158	22
Syphacia montana YAMAGUTI, 1943	35	—	—
Capillaria hepatica (BANCROFT, 1893)	19	2	—
Trichuris sp.	11	—	—
Trematoda			
Plagiorchis muris TANABE, 1922	7	1	7
Cestoda			
Paranoplocephala omphalodes (HERMANN, 1783)	—	8	2
Coronacanthus apodemi (YAMAGUTI, 1954)	—	30	—
Strobilocercus fasciolaris (BATSCH, 1786)	—	3	—
Cladothyridium sp.	2	—	1
Cysticercus sp.	—	1	—

*1 Total number of cases examined
*2 Description appeared in the preceding paper[5)]

TABLE 2 *Relationship between hosts and number of helminth species*

HOST SPECIES	NUMBER OF HELMINTH SPECIES 1	2	3	4	5	None	TOTAL
Clethrionomys rufocanus	72*	43	25	2	1	22	165
Apodemus argenteus	16	109	39	13	1	5	183
Apodemus speciosus	32	28	3	0	0	4	67

* Number of cases infected

Examinations of the stomach content of animals in this study also revealed these facts. The two *Apodemus* take seeds and insects, although they show a different preference, viz., more insects in the former and more seeds in the latter. Besides, it is well known that the intestines of *Clethrionomys* and *Apodemus* are quite different from each other anatomically. Indeed, *C. rufocanus* takes fibrous green materials as foods throughout the year.

As for the absence of adult cestodes in *Clethrionomys* in Hokkaido, it seems to originate in its herbivorous habit. Infection with *Paranoplocephala*, however, is very common in other species of *Clethrionomys* in other places of the world. For example, MOZGOVOI et al. (1966) reported 2% infection rate of *C. glareolus* with *P. omphalodes* in Poland, and RUPES (1964) did 8% of the same host with the same cestode. Discoveries of cestodes of Hymenolepididae from *Clethrionomys* have been also published by many ivestigators. TENORA (1967) found 44% of *C. glareolus* positive for *Hymenolepis horrida* (LINSTOW, 1900) and KINSELLA (1967) reported a 28% incidence of the same cestode in *C. gapperi* in western Montana, U.S.A. According to KOSHKINA (1957), *C. rufocanus* is much more herbivorous than the other species of *Clethrionomys.* From this point of view, the author presumes that the lack of adult cestode species in *Clethrionomys* in Hokkaido is due to less chance of taking arthropod intermediate hosts. He would like also to explain by food habit the existence of different infection rates of cestodes between *A. argenteus* and *A. speciosus.*

Heterakis spumosa and *Plagiorchis muris* are known as cosmopolitan parasites of murid rodents, but *Mammaniduloides hokkaidensis* is limited to Hokkaido. The last species was described by OHBAYASHI et al. (1968) from the same three hosts as in this paper. Recently, in the course of the present study, the author found this nematode from *Sorex unguiculatus* DOBSON (unpublished data). Consequently, it appears that this nematode has a remarkable wide host range.

Further ecological study of *Syphacia emileromani* is required, since the difference in its incidences between *A. argenteus* and *A. speciosus* is not apparent.

B Differences of helminth fauna by age and sex of hosts

Many experimental studies have revealed that helminth infection is greatly influenced by the age and sex of the host. In natural cases, however, it is difficult to know the real age of the host animals. In the present study, with the cooperation of the Hokkaido Group of Field Mouse Research, the age criteria of the voles were assessed on the basis of the development of their molars.

In this chapter, the corresponding real state of each age-type of the voles is shown (tab. 3), and the relationship between the age-types and number of

TABLE 3 *Age criteria of voles (range in days)*

HOST SPECIES	AGE TYPES				
	I	II	III	IV	V
*Clethrionomys rufocanus**1	Less than 80	80∼130	130∼170	200∼300	More than 300
Apodemus argenteus & *A. speciosus**2	Less than 25	30∼ 60	60∼120	120∼300	More than 300

*1 According to ABE (1966, unpublished data)
*2 According to FUJIMAKI (1966) and HIRAIWA (1958)

helminth species is listed (tabs. 4 & 5). Furthermore, the incidences and intensities of the helminth species in each age-type are compared (figs. 1∼8). On the other hand, the occurrence of each helminth is discussed in connection with the sex difference of the hosts.

1 Age of hosts and helminth fauna

Clethrionomys rufocanus The general incidence of infection was low in age-type I. The number of helminth species in positive cases showed a remarkable increase with the progress of age. It can be seen that the older hosts harbored more than two helminth species (tab. 4).

TABLE 4 *Relationship between age types and number of helminth species in Clethrionomys rufocanus (number of cases)*

NUMBER OF HELMINTH SPECIES	AGE TYPES				
	I	II	III	IV	V
None	18	1	3	—	—
1	37	14	9	7	5
2	9	11	10	6	7
3	2	1	6	9	7
4	—	—	—	—	2
5	—	—	1	—	—
Total	66	27	29	22	21

A dominant species in the small intestine was *Heligmosomum yamagutii*. The incidence was 68.1% in type I, gradually increased in parallel with the progress of age, and attained its maximum value (90.5%) in type V (fig. 1). The intensity also increased with the progress of age, 2.2 per host in type I and 8.4 in type V.

A typical increase of incidences related to the age were observed in *Capillaria* *hepatica* and *Mammaniduloides hokkaidensis* (fig. 2). The incidence was low in the younger specimens, but it increased gradually and attained its maximum in type V (28.6% in *C. hepatica* and 42.9% in *M. hokkaidensis*). The intensity of infections, however, was not considered, since the calculation of the number of the former was very difficult and several positive cases for the latter were used in another experiment.

The incidence of *Syphacia montana* increased and attained its maximum value (36.4%) in type IV, but decreased in type V (fig. 3). The intensity was highest in type II and decreased thereafter. The incidence of *Heterakis spumosa* was quite similar to that of *S. montana*, but the intensity reached a miximum in type IV and decreased in type V (fig. 4).

Other helminths of this host were found spontaneously, and the relationships were not considered.

Apodemus argenteus In this animal, only three cases were assigned to type I, of which comparison was restricted. The general incidence was high in all age-types because of a higher incidence of *Longistriata hokkaidensis* and *Syphacia emileromani*. The number of helminth species increased with the progress of host age, and multi-infection was remarkable in type V (tab. 5).

TABLE 5 *Relationship between age types and number of helminth species in Apodemus argenteus (number of cases)*

NUMBER OF HELMINTH SPECIES	AGE TYPES				
	I	II	III	IV	V
None	2	—	2	1	—
1	1	1	8	3	3
2	—	17	55	24	13
3	—	2	15	12	10
4	—	—	3	4	6
5	—	—	—	—	1
Total	3	20	83	44	33

A high incidence of *L. hokkaidensis* was observed throughout all age-types (fig. 5). Incidence reached 100% in type II and only minute fluctuations were seen thereafter. The highest intensity, 144 per host, was obtained from type V.

The maximum incidence of *Syphacia emileromani* was 93.1% in type IV, and a slight reduction, 84.8%, was observed in type V. The mean intensity also reached a maximum in type IV, 107.8 per host, but it decreased in type V, 59.9 (fig. 6).

Infection with *Coronacanthus apodemi* and *Paranoplocephala omphalodes* was positive only in older animals (fig. 7). The incidence was 11.8% in *C. apodemi* and 3.5% in *P. omphalodes* in type III. It increased with the progress of host age and attained a maximum in type V; 33.3% in *C. apodemi* and 9.1% in *P. omphalodes.*

Infection with *Mammaniduloides hokkaidensis* was seen only in older animals (fig. 7). The incidence increased with the progress of host age, similar to that in *Clethrionomys rufocanus.*

Apodemus speciosus The host specimens examined were small in number and their population structure by age varied considerably according to age-type; 70% of the cases belonged to type III. Therefore, only the fluctuations of the dominant species, *Longistriata hokkaidensis,* were considered. The incidence and mean intensity of this nematode increased parallel to the progress of host age (fig. 8). Intensity was much higher, but the general pattern of incidence was similar to that in *A. argenteus.* Intensity was 28.8 per host in type I, and 210.0 in type V.

2 Sexes of hosts and helminth fauna

Only one species, *Mammaniduloides hokkaidensis,* seemed to show a slight difference of infection rate in *Clethrionomys rufocanus*; 6 out of 79 males (7.6%) and 13 out of 86 females (15.3%) were positive. However, no significance was proved; the value of difference was $\chi^2_s=1.53$.

3 Discussion

Many authors state that the main cause of sex resistance to helminth infection is estrogen, which lowers susceptibility in mature females (ADDIS, 1946; BECK, 1952; MATHIES, 1959). Most of these results were obtained by experimental studies. In natural cases, however, many workers reported higher incidences and intensities of helminth infection in adult hosts than in the immature hosts. SHARPE (1964) reported that the incidence of *Heligmosomoides dubius* (SCHULZ, 1930) and *Catenotaenia pusilla* GOEZE, 1782, in *Clethrionomys glareolus* were higher in the adult than in the immature hosts. LEWIS (1968) observed that the helminth infection of *Apodemus sylvaticus* was heavier in the adult than in the juvenile hosts captured in Wales, Great Britain.

In studies on natural cases of rodents, the grouping of the host age is very difficult, and usually the specimens are classified only into two types, mature and immature. In this paper, through the adoption of a detailed age classification, accurate relationships between the host age and the helminth infection could be considered.

The increase of incidence and mean intensity of helminth infection related to the progress of host age in *Heligmosomum yamagutii*, *Capillaria hepatica*, *Mammaniduloides hokkaidensis*, *Longistriata hokkaidensis*, *Coronacanthus apodemi* and *Paranoplocephala omphalodes* were shown. Among these helminths, prominent increased infection was confirmed concerning *C. hepatica*, a parasite of the liver, and *M. hokkaidensis*, a parasite of the mammary glands in females and the bulbo-urethral and prostate glands in males. Judging from their tissue parasitism, these nematodes are thought to remain or accumulate by suprainfection, after the establishment of infection, throughout the host's life. On the other hand, none of these helminth species manifested any differences influenced by the sex of the host. Concerning this fact, the author presumes that the increase of incidence and intensity related to the host age is mainly due to the increase of opportunities for infection with the progress of age. The abundance of helminth species in older voles also supports this conclusion, and the rate of multi-infection is lower in younger voles.

Contrary to the above, a decrease of incidence in older host groups was observed in *Syphacia montana*, *Heterakis spumosa* and *Syphacia emileromani*. MATHIES (1959) showed experimentally that there was greater resistance to infection with *Aspiculuris tetraptera* (NITZCH, 1821) by female white mice, and that this phenomenon was a result of the presence of estrogen in mature females. SHARPE (1964) also observed the same phenomenon in natural cases of *Clethrionomys glareolus* and *Apodemus sylvaticus*, of which the infection level of *A. tetraptera* and *Syphacia obvelata* (RUD., 1802) in mature females was lower.

The reduction of incidence in the three nematodes mentioned above was noted in age-type V, but not in the other age-types, although the sexual maturity of the host occurred at age type II. Therefore, this fact cannot be attributable to the sex of the host. The author considers the reduction originated in various factors such as the lack of opportunity for suprainfection, the discharge of helminths, etc.

C Seasonal changes of helminth fauna

As shown in table 6, no specimens of *Apodemus argenteus* and *A. speciosus* were captured in certain months. The specimens of *Clethrionomys rufocanus* varied in number according to the month, but the materials were obtained throughout the year. In *C. rufocanus*, monthy fluctuations in general incidence (fig. 9), the population of hosts in connection with the number of helminth species (fig. 10), and the intensity of *Heligmosomum yamagutii* (fig. 11) were investigated. *H. yamagutii* was found only in this host. As for *Mammaniduloides hokkaidensis*, the monthly incidences in the three host species were shown en bloc (fig. 9), because this nematode was common in these hosts.

TABLE 6 *Seasonal distribution of voles examined (number of cases)*

MONTHS	HOST SPECIES			TOTAL
	Clethrionomys rufocanus	*Apodemus argenteus*	*Apodemus speciosus*	
June	8	10	0	18
July	9	24	2	35
Aug	8	28	26	62
Sept	12	48	11	71
Oct	21	29	10	60
Nov	46	20	12	78
Dec	5	2	1	8
Jan	8	4	0	12
Feb	15	0	0	15
Mar	9	4	0	13
Apr	19	7	1	27
May	5	7	4	16

Changes in connection with five seasonal periods were found in seven helminth species (figs. 12 & 13). In other helminths, no seasonal fluctuations were observed. The classification of seasonal periods applied below was adopted from the classification by Hokkaido Group of Field Mouse Research[21], KINOSHITA et al. (1952) and OTA et al. (1959).

Early summer (June & July) In this period, the population structure of voles by age is established by new-born younger and overwintered older groups. The environmental conditions are suitable for the growth of the infective larvae and eggs of helminths. Therefore, only a few younger voles were free from helminths and all older voles were infected showing high intensity. The general incidence did not decrease as in the autumn. The incidence of *H. yamagutii* was higher than in the autumn, and the incidence of *Plagiorchis muris* increased more than in spring; however, most helminth species showed lower incidences than in the other seasons.

Summer (August) The voles examined showed a composition similar to the preceding period, although the younger, spring-born voles had grown up and the older ones had decreased in number. As all the younger voles were infected, the general incidence in *C. rufocanus* reached 100%. Such a rapid increase of incidence within a short period was explained by the presence of greater chances of helminth infection because of the suitable environmental conditions for eggs and infective larvae. The highest monthly average temperature, 25.8°C, was obtained in this month. The incidence of *Coronacanthus apodemi*, *Plagiorchis muris* and *Heterakis spumosa* reached their maximum in this period. The former two species require invertebrates as the intermediate host, and the high incidence was attributable to the most abundant invertebrates (tab. 7).

TABLE 7 *Number of invertebrate animals collected by sweeping and pit-fall methods in experimental areas*

INVERTEBRATES	NATURAL FOREST				ARTIFICIAL FOREST			
	June	July	Aug	Sept	June	July	Aug	Sept
Arthropoda								
Acarina	—	2	2	—	48	49	18	—
Aranea	39	15	14	3	52	18	18	8
Insecta								
Orthoptera	1	—	5	4	13	4	—	—
Hemiptera	35	7	116	—	8	26	2	—
Lepidoptera	18	1	2	—	10	2	1	—
Coleoptera	54	65	45	106	52	41	136	99
Neuroptera	—	—	—	—	—	1	—	—
Hymenoptera	72	41	37	8	60	42	27	—
Diptera	138	43	17	—	43	42	25	—
Gastropoda	1	2	6	1	1	—	12	1

Autumn (September & October) This period is the reproductive season for voles; many new-born younger voles appear and the older overwintered ones decrease in number. The majority of *C. rufocanus* examined, 66%, were new-born cases and free from helminths, and the general incidence decreased to 66.6% in October. Adult voles became infected with more than two helminth species. The incidence of *Heligmosomum yamagutii* decreased remarkably, but that of *Syphacia montana* increased. Ten different helminth species were recovered from *A. argenteus*. This abundance of helminth species was thought to originate in the infection established in the summer, since this phenomenon was seen in older voles.

Winter (November～February) In this period, some of the spring-born voles were reduced in number by death, and the younger autumn-born voles dominate the population. The home range of the voles is reduced in early winter by the low temperature and the fall of snow; however, after much snow in January and February, the environmental conditions become stable, and the activity of the voles increases under the snow. Though the environmental conditions are unfavorable for the survival of infective larvae and eggs, the general incidence increases very slowly. The incidences of *Syphacia montana*, *Plagiorchis muris* and *Coronacanthus apodemi* decreased in this period. The lowest monthly average temperature, $-10.5°C$, was obtained in January.

Spring (March～May) The population of the voles is composed of only the overwintered older ones. The activity of the voles increases, and this period is also suitable for the growth of infective larvae and eggs of helminths. The general incidence had already attained 100% in February, and it did not show any fluctuation. This is a period of supra- and multi-infections, which are especially prominent in April and May. Most of the *Clethrionomys* harbored two or more helminth species. The incidence of other species also increased in this period; *Capillaria hepatica*, *Mammaniduloides hokkaidensis* and *Syphacia montana* attained their maximum values.

LEWIS (1968) reported the seasonal variations of parasites of *Clethrionomys glareolus* and *Apodemus sylvaticus* in Aberystwyth and the Skomer Islands, Great Britain. He concluded that 3 species, one nematode in *C. glareolus*, and one trematode and two nematodes in *A. sylvaticus*, showed seasonal fluctuations. KISIELEWSKA (1971), who distinguished five seasonal periods in the year, also studied *C. glareolus* in Poland and found the seasonal differences in helminth fauna.

In the present study, 7 helminth species, *Heligmosomum yamagutii*, *Syphacia montana*, *Heterakis spumosa*, *Capillaria hepatica*, *Mammaniduloides hokkaidensis*, *Plagiorchis muris* and *Coronacanthus apodemi*, manifested seasonal fluctuations. Some of the seasonal changes of the helminth fauna can be explained also by changes in the age composition of the vole population. The three helminth species, *H. yamagutii*, *C. hepatica* and *M. hokkaidensis*, exhibited a typical increase of infection parallel to the progress of host age (fig. 12). A closer relation to host age was recognized in *H. yamagutii*, the dominant species in *C. rufocanus*; a higher incidence was observed except for in very young voles. The fluctuations in the helminth species is considered to be greatly affected by the ratio of younger hosts to the total population.

The remaining 2 species, *C. hepatica* and *M. hokkaidensis*, are tissue parasites, and their higher incidences were recognized only in the older voles (fig. 2). Besides, the highest incidences were seen only in the seasonal period when the population consisted mainly of older voles.

Contrary to the above, *S. montana*, *H. spumosa*, *C. apodemi* and *P. muris* did not show typical increases in relation to host age (fig. 13). Especially in *P. muris*, no relation to host age was observed. The higher incidences of these species in limited periods suggest that the infection is greatly affected by environmental factors or host behavior. A close relationship between the increase of host activity and helminth infection is presented by *C. apodemi* and *P. muris*. It can be said that their highest incidences are limited to the season when invertebrates are abundant, since both the species require an intermediate host. On the other hand, the infection of *S. montana* is established directly, without intermediate hosts. The higher incidences of this nematode in autumn and spring, the reproductive seasons of the hosts, should be explained by the increased opportunity for contact among the various-aged hosts.

The number of voles in each seasonal period is considered insufficient for making a detailed comparison of the dynamics of the helminth fauna. However, the following facts can be stated:—There is a difference in the mode of infection between the spring- and autumn-born voles. The former are easily infected by helminths within a short period after birth, because of the acceleration of suitable environmental conditions for infection. On the other hand, the latter are only rarely infected or free from helminths until the next spring, being affected by unfavorable conditions for the survival and growth of infective larvae toward late autumn to the winter. It must be taken into consideration that the age of hosts and the season of birth are indispensable data for analyzing the helminth fauna of natural cases.

D Differences between helminth fauna by experimental area

Differences between helminth fauna from different areas have been disscussed by many workers. They have usually studied them from the zoogeographical point of view, and the areas examined were separated from each other by long distances. In this paper, however, the voles were captured in two experimental areas, natural forest and artificial forest, which were separated by a distance of only 2 km.

Comparing the helminths from the two areas, differences were observed in 3 species; *Capillaria hepatica* of *Clethrionomys rufocanus*, *Coronacanthus apodemi*

TABLE 8 *Comparison of experimental areas showing incidences of helminths*

HELMINTH SPECIES	NATURAL FOREST		ARTIFICIAL FOREST	
	Occurrence	Incidence %	Occurrence	Incidence %
Capillaria hepatica	2/60*	3.3	17/105	16.2
Paranoplocephala omphalodes	9/142	6.4	1/108	0.9
Coronacanthus apodemi	28/114	24.5	2/69	2.9

* Number of hosts positive/examined

of *Apodemus argenteus* and *Paranoplocephala omphalodes* of *A. argenteus* and *A. speciosus* (tab. 8). The value of the difference χ^2 in *C. hepatica*, *C. apodemi* and *P. omphalodes* was 5.01, 10.65 and 3.37, respectively ($\chi^2_{(1)}$ (0.05)=3.84). Therefore, the abundance of *C. hepatica* in the artificial forest and *C. apodemi* in the natural forest were proved to be significant, but the occurrence of *P. omphalodes* in each area was insignificant.

At the same time, the survey of invertebrate animals in the experimental areas was carried out in the period from June to September, 1967, by members of the Hokkaido Group of Field Mouse Research (tab. 7). As this survey was to investigate the food materials of voles, neither parasitological examination nor taxonomical study of these invertebrates was carried out.

The two helminth species above noted, which revealed significant differences, are known to have a close relationship to arthropods in their life cycles.

C. hepatica is a well-known nematode which requires carnivorous animals for the dissemination of its eggs. However, PAVLOV (1959) proved experimentally that certain saprophagous insects, such as the carrion beetle, *Nicrophorus vespilloides*, could play the role of disseminator. *C. apodemi*, of which the intermediate host is still unknown, belongs to the Hymenolepidinae, and the intermediate hosts might be arthropods.

The survey of invertebrates revealed an abundance of acari in the artificial forest, but the number of coleopterous insects did not show any significant difference between the two areas. This survey did not include parasitological and taxonomical examinations, so it did not explain the different occurrences of *C. hepatica* and *C. apodemi* in the two areas.

The two experimental areas exist within the same forest and are only 2 km distant each other, but the vegetation is very different in each. The artificial forest is predominated by *Abies sachalinensis* and *Fraxinus mandshurica*, planted in 1957, and the dominant undergrowth plant is *Sasa senanensis*. The natural forest is also predominated by *A. sachalinensis*, but the dominant undergrowth plants are *Daphniphyllum humile* and *Polustrichum tripteron*. Considering these differences in vegetation, it may be supposed that there exist more differences in arthropod fauna between the two areas, although no detailed data are presented.

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FIGURE 1 *Incidence and intensity of Heligmosomum yamagutii in Clethrionomys rufocanus*

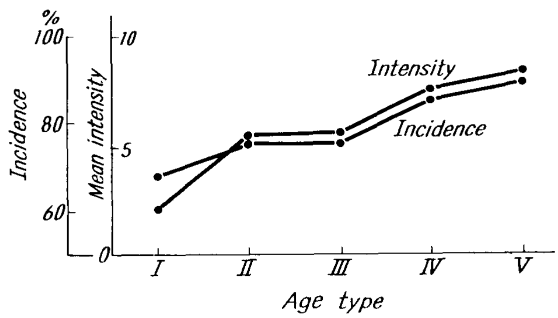

FIGURE 2 *Incidences of Capillaria hepatica and Mammaniduloides hokkaidensis in Clethrionomys rufocanus*

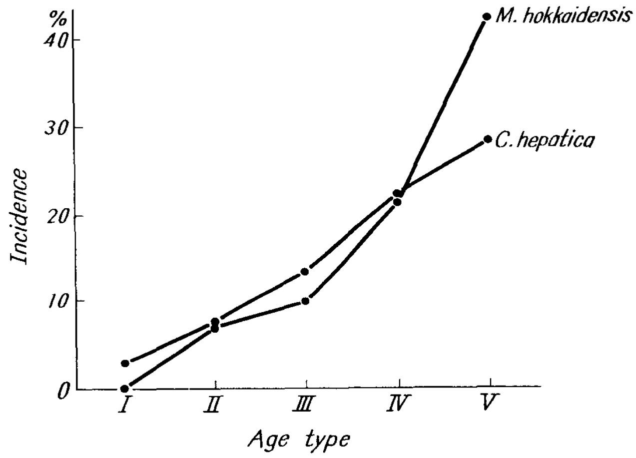

FIGURE 3 *Incidence and intensity of Syphacia montana in Clethrionomys rufocanus*

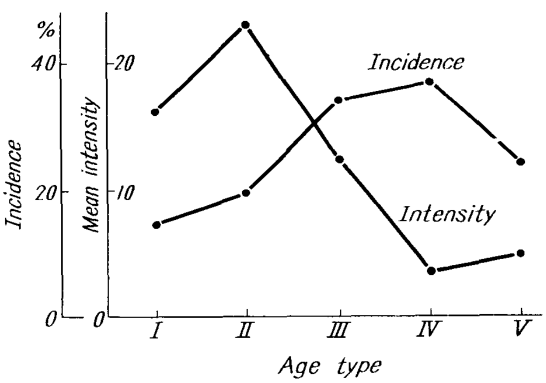

FIGURE 4 *Incidence and intensity of Heterakis spumosa in Clethrionomys rufocanus*

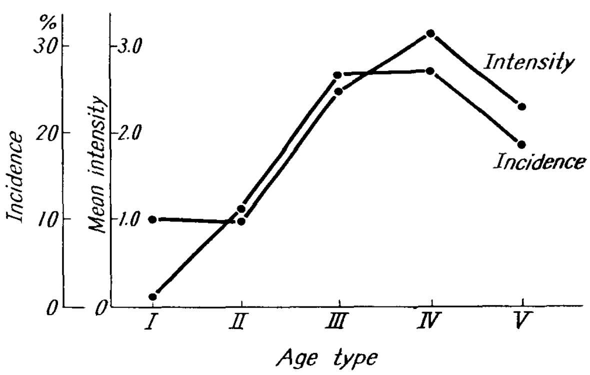

FIGURE 5 *Incidence and intensity of Longistriata hokkaidensis in Apodemus argenteus*

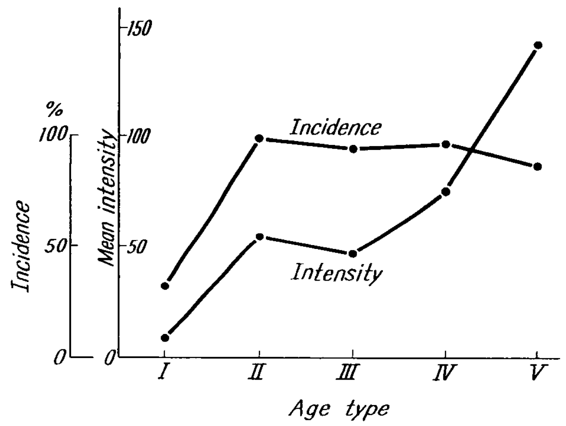

FIGURE 6 *Incidence and intensity of Syphacia emileromani in Apodemus argenteus*

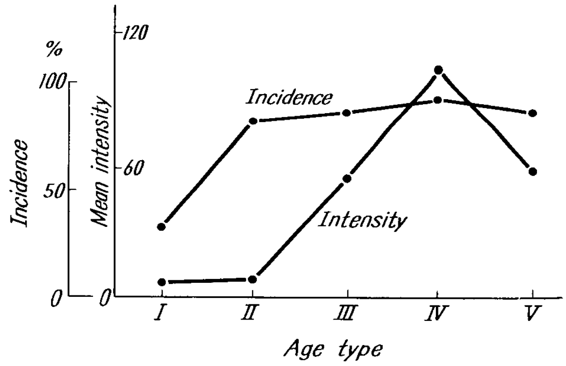

FIGURE 7 *Incidences of Coronacanthus apodemi, Mammaniduloides hokkaidensis and Paranoplocephala omphalodes in Apodemus argenteus*

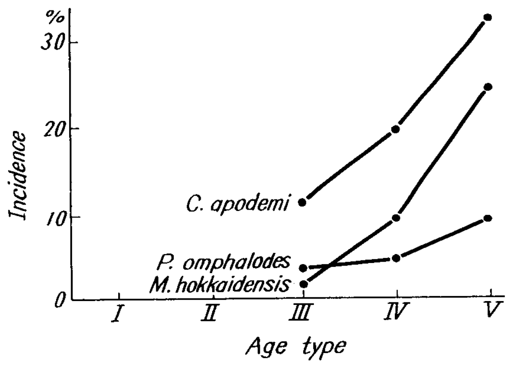

FIGURE 8 *Incidence and intensity of Longistriata hokkaidensis in Apodemus speciosus*

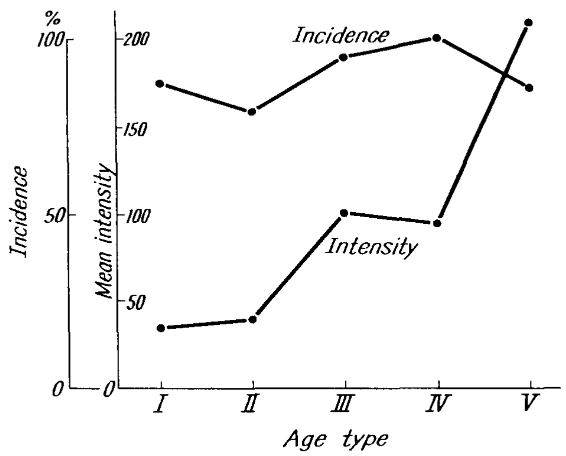

FIGURE 9 *Seasonal fluctuation of general incidence of Clethrionomys rufocanus and incidence of Mammaniduloides hokkaidensis in C. rufocanus, Apodemus argenteus and A. speciosus*

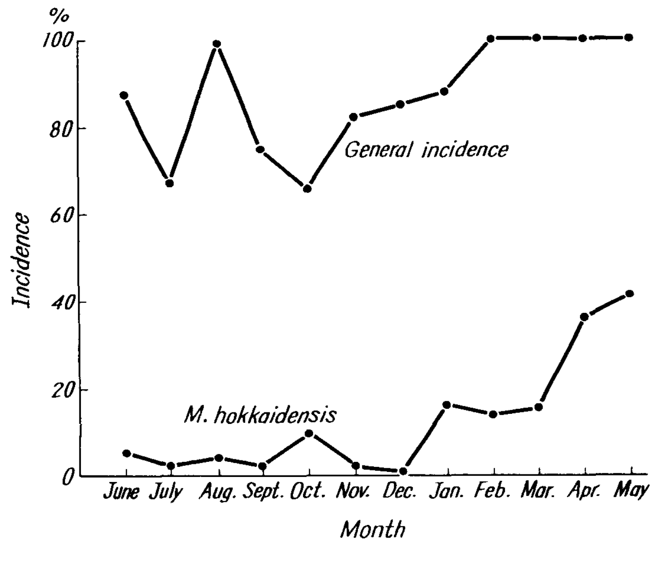

FIGURE 10 *Seasonal changes of the number of helminth species in Clethrionomys rufocanus*

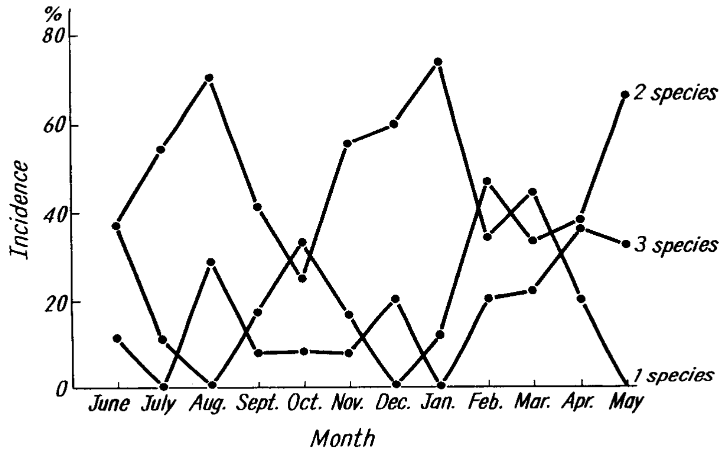

FIGURE 11 *Seasonal fluctuation of intensity of Heligmosomum yamagutii in Clethrionomys rufocanus*

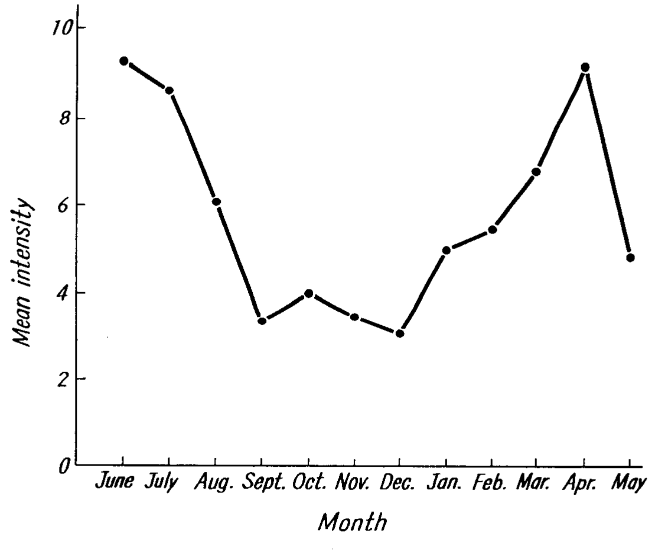

FIGURE 12 *Seasonal changes of incidence of helminthus in Clethrionomys rufocanus (I)*

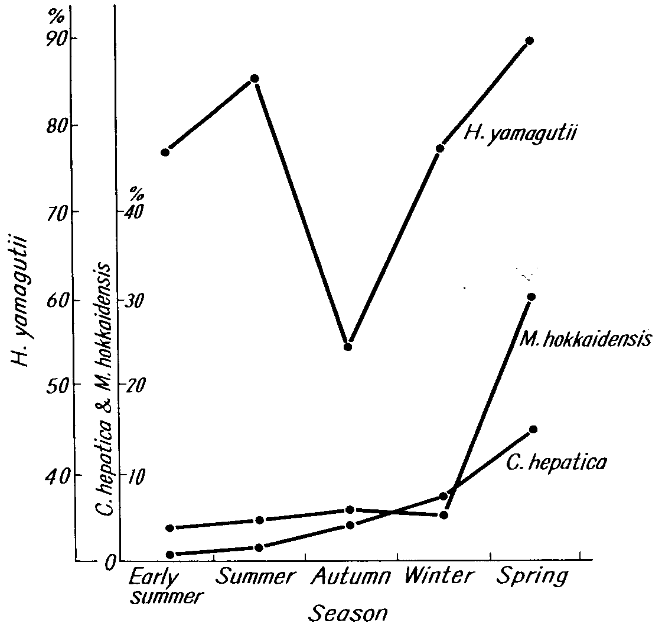

FIGURE 13 *Seasonal changes of incidence of helminths in Clethrionomys rufocanus (II)*