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THE ECOLOGY OF *ECHINOCOCCUS MULTILOCULARIS* (CESTODA: TAENIIDAE) ON ST. LAWRENCE ISLAND, ALASKA. II. — HELMINTH POPULATIONS IN THE DEFINITIVE HOST

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SUMMARY

The helminths of 1,579 arctic foxes from St. Lawrence Island were investigated by standard methods. The foxes, obtained mainly during the winter from fur trappers, harbored 22 species of helminths. Four of those were trematodes, viz., *Maritrema afanassjewi* Belopol'skaia, 1952, *Orthosplanchnus pygmaeus* Iurakhno, 1967, *Plagiorchis elegans* (Rudolphi, 1802) and *Alaria marcianae* (LaRue, 1917), each of which occurred in a single host. Two species of cestodes, *Diphyllobothrium dendriticum* (Nitzsch, 1824) and *Mesocestoides kirbyi* Chandler, 1940, were uncommon (in 2.7 and 1.3 % of the foxes, respectively). *Taenia polyacantha* Leuckart, 1856 and *Echinococcus multilocularis* Leuckart, 1863 were present in about 80 % of the foxes, and *Taenia crassiceps* (Zeder, 1800) in less than 10 %. The specimens of *Taenia* spp. from the autumn-winter sample were usually destrobilate. In about 2 % of the foxes, acanthocephalans of six species occurred. Four of those, of the genus *Corynosoma* Lühe, 1904, were common in marine mammals of the region; a fifth, *Corynosoma clavatum* Goss, 1940, has been reported previously only from marine birds of the Southern Hemisphere; and the sixth, *Polymorphus* cf. *minutus* (Goeze, 1782), has been found widely in waterfowl of the Northern Hemisphere. Of the nematodes, *Sobolophyme baturini* Petrov, 1930, *Cylicospirura felineus* (Chandler, 1925), and *Physaloptera* sp. were rare (with each in only one to three foxes). *Trichinella nativa* Boev et Britov, 1972 and *Crenosoma vulpis* (Dujardin, 1844) were uncommon (1.5 and 4 %, respectively). The nematodes most often present were *Toxascaris leonina* (von Linstow, 1902) (89 %) and *Uncinaria stenocephala* (Railliet, 1884) (40 %). Several of the rare to uncommon helminths probably were transported to the island by foxes immigrating from the adjacent continents via the pack ice.

RÉSUMÉ : **Écologie d'*Echinococcus multilocularis* (Cestoda : Taeniidae) dans l'île Saint-Laurent (Alaska). II. Populations helminthiques des hôtes définitifs.**

Les helminthes de 1 579 renards arctiques de l'île Saint-Laurent ont été examinés par des méthodes standards. Les renards obtenus, principalement pendant l'hiver, de trappeurs de fourrures, donnaient asile à 22 espèces d'helminthes. Quatre trématodes, *Maritrema afanassjewi* Belopol'skaia, 1952, *Orthosplanchnus pygmaeus* Iurakhno, 1967, *Plagiorchis elegans* (Rudolphi, 1802) et *Alaria marcianae* (LaRue, 1917), étaient présents chacun dans un seul hôte. Deux cestodes, *Diphyllobothrium dendriticum* (Nitzsch, 1824) et *Mesocestoides kirbyi* Chandler, 1940, étaient peu communs (dans 2, 7 et 1,3 % des renards, respectivement). *Taenia polyacantha* Leuckart, 1856 et *Echinococcus multilocularis* Leuckart, 1863 étaient présents dans à peu près 80 % des renards, et *Taenia crassiceps* (Zeder, 1800) dans moins de 10 %. Les spécimens de *Taenia* spp. étaient généralement déstrobilés. Six espèces d'Acanthocéphales sont présentes dans à peu près 2 % des renards. Quatre du genre *Corynosoma* Lühe, 1904, étaient communes dans les mammifères marins de la région. Une cinquième, *Corynosoma clavatum* Goss, 1940, a été signalée auparavant seulement dans les oiseaux marins de l'Hémisphère Sud et la sixième, *Polymorphus* cf. *minutus* (Goeze, 1782), a une vaste répartition chez les oiseaux aquatiques de l'Hémisphère Nord. Les nématodes *Sobolophyme baturini* Petrov, 1930, *Cylicospirura felineus* (Chandler, 1925), et *Physaloptera* sp. étaient rares; ils se trouvaient dans seulement un à trois renards chacun. *Trichinella nativa* Boev et Britov, 1972 et *Crenosoma vulpes* (Dujardin, 1844) étaient également peu communs (1,5 et 4 % respectivement). Les plus communs des nématodes étaient *Toxascaris leonina* (von Linstow, 1902) (89 %) et *Uncinaria stenocephala* (Railliet, 1884) (40 %). Plusieurs des espèces rares ou peu communes ont été probablement importées dans l'île par des renards immigrants des continents adjacents par la banquise.

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Echinococcus multilocularis Leuckart, 1863, the causative agent of alveolar hydatid disease in man, has been investigated widely in the Arctic (Rausch, 1967, 1986). Its ecology has been studied most intensively on St. Lawrence Island (SLI), which is situated in the northern part of the Bering Sea, 250 km south of Bering Strait. In those studies during 1950 to 1955, the life-cycle of *E. multilocularis* was found to involve a rodent as intermediate host and the arctic or polar fox, *Alopex lagopus* (L.), and sledge dog, *Canis lupus* f. familiaris L., as the definitive hosts (Rausch and Schiller, 1951, 1954; Rausch, 1952 *a*). Because the primary thrust of those studies concerned *E. multilocularis* as a specific pathogen with a distinct cycle (Rausch and Schiller, 1956), the other helminths found in the respective hosts usually were not reported, but were preserved for later study. A large amount of additional material was acquired later (1956 to 1973), during a phase of concentrated ecological investigations (Fay, 1973). The purpose of this paper is to report on the total helminthic fauna from all of the foxes we examined on SLI and to compare our findings with those from arctic foxes elsewhere.

STUDY AREA

The characteristics of the environment on SLI have been described previously in detail, e. g., by Rausch (1953 *a*), Rausch and Schiller (1956), Fay and Cade (1959), Hughes (1960), and Fay (1973). To recapitulate briefly, the 5,000 km^2 island is snow-covered and surrounded by the pack ice of the Bering Sea from December to May. High winds and blowing snow are common from October to June, and fog and drizzle are frequent during the summer. Since the permanently frozen subsoil restricts the percolation of water, about 60 % of the surface of the island is wet, sedge-*Sphagnum* tundra, and the rest is about equally divided between rocky habitats and shallow lakes and lagoons. Arborescent vegetation is absent.

The indigenous mammals of the island are the arctic fox, the arctic ground squirrel, *Citellus parryi* (Richardson), the northern or root vole, *Microtus oeconomus* (Pallas), the northern red-backed vole, *Clethrionomys rutilus* (Pallas), the varying lemming, *Dicrostonyx exsul* Allen, and the masked shrew, *Sorex jacksoni* Hall et Gilmore (Rausch, 1953 *a*). The foxes prey on the four rodents, as well as on a wide variety of nesting birds in the summer, and they apparently store voles and birds in large quantities for use during the winter. Nonetheless, their primary source of food in winter is carrion, mainly consisting of beach-cast marine mammals and benthic invertebrates (Fay and Stephenson, 1989).

The young foxes are born, in litters averaging about 10, in June and remain at the den throughout the summer. They become independent by October and reach adult size and sexual maturity by the following spring (Fay *et al.*, manuscript). The fox population fluctuates in size from year to year and frequently is depleted and/or augmented by exodus of foxes onto the pack ice and influx from the ice during the winter. Arctic foxes are well known as long-distance travellers over both ice and land (Wrigley and Hatch, 1976; Eberhardt and Hanson, 1978; Garrott and Eberhardt, 1987), so those reaching the island *via* the pack ice may come from both the Eurasian and North American continents. Such dispersing foxes also transport helminths and microorganisms. For example, a female fox that was killed on « Ice Island T-3 », when it was in the Arctic Ocean about 900 km from shore (3 XII 66), harbored *Echinococcus multilocularis* and *Taenia* spp. that could only have been acquired on the continents or major islands. Also, the virus of rabies was isolated from its brain.

MATERIALS AND METHODS

Nearly all of the foxes examined were received as frozen carcasses from which the pelt had been removed. These had been trapped by the residents of SLI from mid-November to mid-April each year. A few others were collected by us in other months. The trapped animals were shipped to the Arctic Health Research Center in Anchorage (in Fairbanks after 1966), where they were stored frozen for up to three months before being autopsied. Each fox was processed primarily for investigation of its helminths. We also took standard measurements, preserved the skull, and examined the reproductive organs and gastric contents, as reported elsewhere (Fay and Stephenson, 1989; Fay *et al.,* manuscript).

Each fox was assigned an accession number, and all data pertaining to the animal and materials preserved from it were recorded in reference to that number. Date of death and locality were recorded at time of capture; other information was added as the examinations progressed. In the laboratory, each carcass was allowed to thaw overnight (about 15 hr) at a temperature of 15° C. After the morphometric data were recorded, the skull was removed and cleaned for use in age-determination. The body cavities were opened, the viscera removed, and each organ was examined separately. The lungs were palpated and examined for external lesions, after which the trachea, bronchi, and bronchioles (as small as 2-3 mm in diameter) were opened with scissors and searched for lungworms. A 2- to 3-gram sample of diaphragm was obtained for examination (press-method) for larvae of *Trichinella.* After external examination, the liver was sliced in several places and the cut surfaces examined as well. The stomach also was examined externally, then opened and the contents cleaned and preserved for identification of food-items and collection of any nematodes. The intestine was opened full-length with scissors, the contents stripped by means of pressure between thumb and forefinger (to dislodge any attached helminths), and the mucosal surface was inspected. The intestinal contents were rinsed in several changes of tapwater, after which all helminths were isolated and fixed in a 10 % solution of formalin and stored until removed for identification.

Identification of species of *Taenia* was based on shape of the rostellar hooks (Rausch, 1952 *b,* 1959; Schiller, 1953). Specimens lacking hooks (and destrobilate as well) were recorded as « unidentified ».

The helminths from most of the foxes were counted, except that counting usually was not attempted for *E. multilocularis* because of its large numbers. The relative size of populations of that cestode was assessed, however, in a subjective way as low or light (« L »), medium (« M »), and heavy or severe infections (« H »). Actual ranges of numbers in those categories were determined by direct counts and from aliquots drawn from a nonselected subsample of foxes.

Finally, the age of each fox was determined from dental characters, as described elsewhere (Fay *et al.,* manuscript).

Statistical handling of the summarized data was mainly by means of the 2-sample *t*-test and the Chi-squared 2 × 2 table, applying Yates correction where appropriate for small samples.

RESULTS

We examined 1,579 arctic foxes from SLI. Most of the animals were taken during the prescribed annual trapping season, mid-November to mid-April; the majority was obtained during December. Twenty-one (1 %) of the foxes had no helminths. From the remaining 1,558 animals, helminths of 22 species were recorded in various combinations. Date of death of the host is indicated below in parentheses for the uncommon species of helminths.

I. Trematoda

Trematodes representing four species were found in just four of the foxes.

Maritrema afanassjewi Belopol'skaia, 1952. One young fox (2 XII 55) harbored a single specimen. *M. afanassjewi* is a common intestinal trematode in arctic foxes farther south in the Bering Sea [e. g., Commander Islands (Afanas'ev, 1941); Aleutian Islands (Fay and Williamson, 1962); Pribilof Islands (Fay and Williamson, 1962)]. It occurs in other mammals as well, and in birds of various species (Rausch *et al.,* 1979). The metacercarial stage has been found in marine amphipods of the species *Orchestia ochotensis* Brandt (Tsimbaliuk *et al.,* 1968).

Orthosplanchnus pygmaeus Iurakhno, 1967. Four specimens were obtained from a single fox (15 XII 56). Described from a gray whale, *Eschrichtius robustus* (Lilljeborg), from the Chukchi Sea, this trematode is known otherwise only from a ringed seal, *Phoca hispida* Schreber, collected near Gambell, SLI (Adams and Rausch, 1989). All specimens of *O. pygmaeus* have been found in the small intestine of the host, whereas other species of the genus usually inhabit the gall bladder and the bile ducts. The intermediate hosts are unknown. Voucher specimens from arctic fox: USNM Helm. coll. No. 81 314.

Plagiorchis elegans (Rudolphi, 1802) (syn. *P. massino* Petrov et Tikhonov, 1927). One fox (XII 52) harbored a single specimen. This trematode, morphologically quite variable, occurs widely in birds and mammals in the Holarctic but appears to be generally uncommon in carnivores. An unusually high prevalence (45 %), however, has been reported from arctic foxes in Greenland (Rausch *et al.,* 1983). We collected a specimen of *P. elegans* also in a dog at Gambell, SLI (31 XII 51). In the Chaunsk Lowlands of Chukotka, metacercariae have been found in chironomids (*Chironomus* sp.) by Orlovskaia and Kontrimavichus (1975).

Alaria marcianae (LaRue, 1917) (for synonyms, see Dubois, 1982). One fox (7 XII 58) had twelve specimens in the small intestine. *A. marcianae* is a rather common trematode in red foxes, *Vulpes vulpes* (L.), and other canids on the Alaskan mainland. The investigations in Canada by Pearson (1956) demonstrated that the mesocercariae develop in tadpoles of the wood frog, *Rana sylvatica* Le Conte (second intermediate host). The frog also inhabits the zone of taiga on the mainland of Alaska but is not present on SLI. *A. marcianae* is a nearctic species; *A. alata* (Goeze, 1782) occurs in carnivores in the Soviet Union and elsewhere in Eurasia, but evidently it has not been reported from the arctic fox (Kozlov, 1977). Voucher specimens: USNM Helm. Coll. No. 81 315.

II. Cestoda

Cestodes make up a major component of the helminthic fauna of the arctic fox throughout its range. With the exception of a relatively uncommon diphyllobothriid, all of the species of cestodes recorded from *A. lagopus* on SLI have a mammalian intermediate host.

Diphyllobothrium dendriticum (Nitzsch, 1824). Cestodes of the genus *Diphyllobothrium* Cobbold, 1858 occurred in the small intestine of 42 (2,7 %) of foxes, in numbers ranging from one to eight strobilae per infected animal ($\bar{x} \pm SD = 2.17 \pm 1.95$, $n = 24$). All were identified as *D. dendriticum,* presumably acquired by the consumption of freshwater fishes. The foxes are known to catch arctic grayling, *Thymallus arcticus* (Pallas), and we have repeatedly found plerocercoids in that fish, as well as in Dolly Varden trout, *Salvelinus malma* (L.), on the island (Fay and Stephenson, 1989 and unpublished data).

D. dendriticum (originally reported as *Diphyllobothrium* sp.) also was found in 7 (32 %) of 22 arctic foxes on St. Matthew Island, Bering Sea, where Dolly Varden trout were abundant in brackish and freshwater lakes (Rausch and Rausch, 1968). Four (10 %) of 38 foxes from western Greenland were infected (Rausch *et al.,* 1983), and Serdiukov (1979) listed the arctic fox as a host of *D. dendriticum* in western Siberia. Gubanov (1964) reported *D. ditremum* (Creplin, 1825) from that host in Iakutiia. Otherwise, identifications from foxes have been reported as *D. latum* (Linnaeus, 1758) (probably erroneous) or as *Diphyllobothrium* sp.

On SLI, *D. dendriticum* was present more often in foxes taken in summer and autumn (4/27 in August to November) than in winter and spring (38/1 495 in December to May ($X^2_{(1)} = 10.665$, $p < 0.005$), which probably is a reflection of the short life-span of the cestode and of the greater availability of fishes in the warmer months than in winter, when the island's lakes and rivers are ice-covered.

Taenia polyacantha arctica Rausch et Fay, 1988 (syn. *Monordotaenia alopexi* Obushenkov, 1983; *Tetratirotaenia polyacantha* (Leuckart, 1856) Abuladze, 1964, in part) and *Taenia crassiceps* (Zeder, 1800) (syn. *Taenia hyperborea* von Linstow, 1905). Cestodes of the species *T. polyacantha* and *T. crassiceps* were among the most common inhabitants of the small intestine of the SLI foxes, occurring in 1,446 (92 %) of the animals examined and ranging in numbers from one to 722 specimens per infected fox

($\bar{x} \pm SD = 42.2 \pm 67.49$ cestodes in 1,067 infected foxes). Only the *arctica* subspecies of *T. polyacantha* was represented.

T. polyacantha was present about ten times more often than was *T. crassiceps* (85 % versus 7 % in 1,200 foxes) and occurred in larger numbers as well ($\bar{x} \pm SD = 34.2 \pm 53.99$ cestodes for 1,019 populations of *T. polyacantha* versus 19.7 ± 44.97 cestodes for 87 populations of *T. crassiceps*; $t = 2.834$, $p < 0.025$). The specimens of both species were usually destrobilate in winter-caught foxes (*i. e.,* in 674 of 779 infected animals in December); fully developed strobilae were common in the foxes only in summer and autumn (8 of 15 in August to November) ($X^2_{(1)} = 20.02$, $p < 0.001$). We judged that destrobilation took place in autumn, perhaps as a consequence of the shift in the foxes' diet at that time, from living prey to mainly carrion (Fay and Stephenson, 1989).

T. polyacantha and *T. crassiceps* are acquired by the foxes through the consumption of arvicoline rodents that serve as the intermediate hosts. The northern vole, which is the most abundant arvicolid on the island, infrequently harbored the cysticerci of those taeniids (0.9 % of 6,508 voles). Of the 60 voles infected, only one had cysticerci of *T. crassiceps*; the other 59 had *T. polyacantha.* Neither species was found in 62 red-backed voles from the northwestern part of the island, but each of 7 red-backed voles obtained near Savoonga, on the north-central coast, in June 1989 was infected with *T. crassiceps.* We also found cysticerci of *T. crassiceps* in one of 13 varying lemmings. The varying lemmings and red-backed voles are uncommon prey of arctic foxes on the island (Fay and Stephenson, 1989).

The number of cysticerci of *T. polyacantha* in the northern voles ranged from one to 65 ($\bar{x} = 23.8$ for 38 voles), about 85 % of which were viable and infective (Rausch and Fay, 1988 and unpublished data). Hence, for more than 90 % of the foxes to have become infected with an average of 42 *T. polyacantha* each, the mean intake of northern voles necessarily would have been more than 200 voles per fox in the previous few months.

Taenia crassiceps and *T. polyacantha* occur in arctic foxes on other islands in the Bering Sea, as well as throughout the holarctic zone of tundra, but their relative abundance varies regionally. On Nunivak Island, we found those taeniids in 85 % of 33 foxes, and *T. polyacantha* was by far the more common there, as on SLI. Von Linstow (1905) described *T. hyperborea* (= *T. crassiceps*) from foxes of the eastern coast of Greenland, where the varying lemming, *D. groenlandicus* (Traill), was the only available intermediate host. Farther west, on Banks Island, Canada, *T. crassiceps* was found in 78 % of 50 foxes, and *T. polyacantha* was absent (Eaton and Secord, 1979). Along the northern coast of Alaska, *T. crassiceps* was slightly the more common of the two, occurring in 83 % of 104 arctic foxes examined by us; *T. polyacantha* was present in 71 % of those animals. In Chukotka, Ovsiukova (1967) examined 178 foxes, 27 % of which were infected by *T. crassiceps* and only 1 % by *T. polyacantha.* To the west, in Iakutiia, only *T. crassiceps* was present in 25 % of 169 animals examined by Gubanov (1964). Still farther to the west, on the Iamal Peninsula, Luzhkov (1963) found 47 % of 118 foxes infected by *T. crassiceps* and 86 % by *T. polyacantha.*

Echinococcus multilocularis Leuckart, 1863 (syn. *Echinococcus sibiricensis* Rausch et Schiller, 1954; *Alveococcus multilocularis* (Leuckart, 1863) Abuladze, 1964). This cestode occurred nearly as commonly as *Taenia* spp. and in much greater numbers. The overall mean rate of infection was about 77 % in the 1,579 foxes, but prevalences ranged upward to ca. 100 % seasonally (Fay and Rausch, 1966). Numbers per infected host ranged from one to more than 180,000 cestodes in the 138 animals for which entire populations were counted.

We classified the relative intensity of the infections in nearly 1,100 foxes at the time of autopsy (as noted): L (light infections); M (moderate); and H (heavy). Although the means of our subsequent counts for verification did show a clear gradient *(table I),* only the means of categories L and M differed significantly from each other ($t = 5.34$, $p < 0.001$); the means for M and H were more similar ($t = 1.30$, $0.10 < p < 0.25$).

TABLE I. — *Numbers of* E. multilocularis *per fox, in relation to estimated relative intensity of infection.*

Estimated relative intensity	*No. of foxes*	*Number of strobilae per host*		
		Range	*Mean*	*SD*
L	79	1- 60,350	7,399	12,078.8
M	40	120-184,200	43,750	42,198.5
H	19	966-157,150	58,975	47,070.3

The northern vole is the important intermediate host of *E. multilocularis* on SLI. Rates of infection in it by the larval cestode generally are less than 10 % but may exceed 80 % locally. Red-backed voles and shrews also have been found infected, but they appear to have little significance in the cycle. The red-backed voles seldom are eaten (Fay and Stephenson, 1989), and we have no indication that the shrews are ever consumed by the foxes.

In the zone of tundra, *E. multilocularis* has a nearly circumpolar distribution. The first indication of its occurrence in northeastern Siberia was the report by Kruzenshtern' (1892) of alveolar hydatid disease in Iakutiia. It is now known to be present in the Eurasian tundra from the White Sea to Bering Strait (Rausch, 1967). After the cestode was recorded on SLI in 1950, it was found in arctic North America, including some islands of the Canadian

Arctic Archipelago. Numerous surveys conducted since 1957 in Eurasia have shown that prevalence in the arctic fox there frequently is high: Ovsiukova (1966) found 34 % of 178 foxes in Chukotka infected; Obgol'ts *et al.* (1980) reported 77 % of 86 foxes on the Taimyr Peninsula to be infected; and Isakov (1982) found 36.8 % of 685 foxes in Iakutiia infected. The variation of infection rates in the foxes of SLI, relative to parasite-host interactions, was outlined briefly by Fay and Rausch (1966) and will be discussed in detail in a subsequent report.

Mesocestoides spp. Cestodes of the genus *Mesocestoides* Vaillant, 1863 were uncommon in our sample, occurring in only 21 foxes (1.3 %). Of the 13 foxes for which numbers of strobilae were recorded, nine harbored one or two, and four contained 19, 21, 68 and 130. The cestodes possibly had been acquired locally, although we never found tetrathyridia in any of several thousand potential mammalian and avian hosts that we examined on the island.

Only *Mesocestoides kirbyi* Chandler, 1944 was identified from foxes on SLI (Shults, 1970) (but not all of the specimens were studied). That species is a component of the helminth faunas in various carnivores on the Alaskan mainland and has been recorded from the arctic fox and other mammals in the Soviet Far East by Chertkova and Kosupko (1978). *M. lineatus* (Goeze, 1782) also might be expected in foxes on SLI, since it is widely distributed in Eurasia and North America; it has been identified from arctic foxes on the Pribilof and St. Matthew Islands, Bering Sea (Shults, 1970). In Chukotka, it was found in 54 % of 178 animals examined by Ovsiukova (1967), and was present in 13 % of 38 foxes from western Greenland (Rausch *et al.,* 1983), as well.

On the mainland of Alaska, we found tetrathyridia of *M. kirbyi* in a northern red-backed vole (24 IX 66) and of *M. lineatus* in shrews, *Sorex cinereus* Kerr and *S. monticolus* Merriam (28 IX 73 and 7 III 76, respectively), collected in the Wrangell Mountains (leg. RLR). Those from the vole and the masked shrew were identified from strobilae reared in dogs. We also found tetrathyridia of *M. lineatus* in one of five Pribilof shrews, *Sorex pribilofensis* Merriam (25 VIII 65) on St. Paul Island (leg. FHF). Comparatively high rates of infection with tetrathyridia of *Mesocestoides* sp. were reported by Gubanov and Fedorov (1970) in rodents of Iakutiia, including 1.1 % in the northern vole , 1.1 % in the northern red-backed vole, and 3.7 % in the red-grey vole, *Clethrionomys rufocanus* (Sundevall).

III. Acanthocephala

Acanthocephalans, mainly representing the genus *Corynosoma* Lühe, 1904, were found in only 34 (2.3 %) of the foxes, in numbers ranging from one to six per fox ($\bar{x} \pm SD = 2.15 \pm 1.60$ in 26 foxes). Most of the species recorded were those we have often collected from marine mammals in the vicinity of SLI; evidently, they can develop in any mammal or bird that ingests the infective stage.

Corynosoma strumosum (Rudolphi, 1802). Numbers from one to three in seven foxes were found in our sample from SLI. We and co-workers also collected it there in a ribbon seal, *Phoca fasciata* Zimmermann (leg. FHF), a spotted seal, *P. largha* Pallas (leg. E. L. Schiller), a sledge dog (leg. ELS), and a pelagic cormorant, *Phalacrocorax pelagicus* Pallas (leg. FHF). On the mainland of Alaska, we found it in other mammals and birds: red fox (at Hooper Bay and Cold Bay); sledge dog (at Tununak); man (twice, at Chevak); glaucous-winged gull, *Larus glaucescens* Naumann (at Napaskiak); thick-billed murre, *Uria lomvia* (L.) (at Point Barrow). Voucher specimens from arctic fox: USNM Helm. Coll. No. 81 316.

Corynosoma semerme (Forssell, 1904). Two specimens of *C. semerme* and one of *C. strumosum* were found in one fox (XII 58), and one of each of those species was present in a second fox (XII 58). Other records of *C. semerme* were from one ribbon seal (leg. FHF) and one spotted seal (leg. ELS). We did not record it in mammals on the mainland of Alaska, but obtained juvenile specimens from a burbot, *Lota lota* L., collected at Tuluksak. Voucher specimens from arctic fox: USNM Helm. Coll. No. 81 317.

Corynosoma validum Van Cleave, 1953. A single specimen was found in one fox. The allotype male of this acanthocephalan was collected on the island from a walrus, *Odobenus rosmarus* (L.) in April 1950 (leg. RLR). Other hosts there were a ribbon seal (leg. J. J. Burns), a spotted seal (leg. ELS), and a sledge dog (leg. ELS) (Five specimens were obtained from the dog, along with two each of *C. clavatum* and *C. villosum,* 28 VI 53). Voucher specimens: that from the fox in the collection of Dr G. D. Schmidt; specimens from a ribbon seal have been deposited, USNM Helm. Coll. No. 81 318.

Corynosoma villosum Van Cleave, 1953. In eight foxes, one to three *C. villosum* were present. The type material of the species was obtained on the island from a Steller sea lion, *Eumetopias jubatus* (Schreber) in August 1950 (leg. ELS). Except for the aforementioned dog, we have no further records of it from SLI. Elsewhere, we found a single adult in a crested auklet. *Aethia cristatella* (Pallas), on Amchitka Island, Aleutian Islands (leg. RLR), and juveniles in an unidentified flounder (Teleostomi: Pleuronectidae) at Seward, Alaska, in August 1958. Voucher specimens from arctic fox: USNM Helm. Coll. nO. 81 319.

Corynosoma clavatum Goss, 1940. We identified *C. clavatum* from four foxes, in numbers from two to five per host, and found it on SLI in addition in the aforementioned dog and in a red-throated loon, *Gavia stellata* (Pontoppidan), which harbored five specimens (leg. FHF). *C. clavatum* has been known previously only from cormorants (Pelicaniformes: Phalacrocoracidae) in Australia and Antarctica (Zdzitowiecki, 1986). Voucher specimens from arctic fox: USNM Helm. Coll. No. 81 320.

Polymorphus cf. *minutus* (Goeze, 1782). six acanthocephalans of the genus *Polymorphus* Lühe, 1911 were found by us in a single fox; it was not recorded from any other animals on the island. Those six resembled the species *P. minutus,* which occurs widely in the northern hemisphere in birds. Gammarids serve as the intermediate host, and juveniles are found in fishes. Voucher specimens from arctic fox: USNM Helm. Coll. No. 81 321.

Additional data concerning some of the acanthocephalans were summarized by Van Cleave (1953). According to Kozlov (1977), only *C. strumosum* and *C. semerme* have been reported from the arctic fox in the Soviet Union. Arctic foxes presumably become infected by acanthocephalans through feeding on marine fishes.

IV. Nematoda

The foxes of SLI were host to seven species of nematodes. An eighth, *Heligmosomum* sp., was found in the intestine of one animal, but we assume that it remained following the consumption of an infected vole. *Heligmosomum nearcticum* Durette-Desset, 1967 occurs commonly in northern voles on the island.

Trichinella nativa Boev et Britov, 1972. The cold-adapted member of the genus *Trichinella* Railliet, 1895, still of uncertain taxonomic status, is present in carnivores throughout the Arctic, but at quite diverse rates of infection. On SLI, we found *T. nativa* in only 10 (1.5 %) of 664 foxes, a finding comparable with Madsen's (1961) in Greenland (1.4 %), but very low compared with data from other northern areas. *T. nativa* was present in two of five arctic foxes we examined from the ice-island T-3 at lat. 74° N, long. 165° W (III 62); in 10 % of 117 from the northern coast of Alaska (Rausch *et al.,* 1956); and in 12 % of 270 from northern and northeastern Siberia (Lukashenko and Brzheskii, 1963). For 1,134 arctic foxes examined in the USSR, Bessonov (1972, p. 60) reported that 15 % were infected.

Sobolophyme baturini Petrov, 1930 (syn. *S. sahalinense* Shimakura et Odajima, 1934). *S. baturini,* a characteristic nematode of mustelids in the holarctic zone of taiga, was recorded from two foxes (2 III 59 and 3 IV 60), which harbored one and two specimens, respectively. The species is common in the marten, *Martes americana* (Turton) on the mainland of Alaska (unpublished data) and in the closely related *M. zibellina* (L.) of Kamchatka (Kontrimavichus and Skriabina, 1963). It has not been reported previously from the arctic fox (Kozlov, 1977). Karmanova (1963) found oligochaetes of the family Enchytraeidae to be the intermediate host of *S. baturini*; paratenic hosts may be involved in transmission to the final host.

Toxascaris leonina (von Linstow, 1902). The most common nematode in the small intestine of the foxes of SLI was *T. leonina,* which occurred seasonally in 79 to 100 % ($\bar{x}$ = 89 %) of them, overall. Numbers per fox ranged from one to 134 ($\bar{x} \pm SD = 10.1 \pm 13.53$ in 399 foxes). In one case, molting larvae were found in the peritoneal cavity. Foxes may become infected through ingestion of embryonated eggs around the dens and perhaps of larvae that often encyst in northern voles (FHF, unpublished data).

Annually, the prevalence of *T. leonina* in the foxes declined from a maximum near 100 % in summer-autumn to a minimum of about 75 % in January; thereafter, the proportion rose again and approached 100 % by April-May.

Physaloptera sp. Nematodes of the genus *Physaloptera* (Rudolphi, 1819) were found only once (3 XII 55); the species was not determined. Any of several species might occur incidentally in the arctic fox. On the Alaskan mainland, we recorded *P. preputialis* von Linstow, 1889 from a red fox from the central part of the Brooks Range (USNM Helm. Coll. No. 56365), and *P. torquata* Leidy, 1889 from wolverines, *Gulo gulo* (L.), from Arctic Village and the Wrangell Mountains (USNM Helm. Coll. Nos. 56170 and 56171, respectively). Kozlov (1977) noted that the common species in northeastern Siberia, *P. sibirica* Petrov et Gorbunov, 1931, is the sole physalopterid recorded there from the arctic fox. *P. sibirica* is common in red foxes of central North America (Rausch and Richards, 1971), but we have not found it in Alaska.

Cylicospirura felineus (Chandler, 1925). Three foxes in our sample contained nematodes of the genus *Cylicospirura* Vevers, 1922 (4 XII 58, 4 II 59, and 9 X 61). The first of those specimens was identified as *C. felineus* (USNM Helm. Coll. No. 56367); the others were not studied. Recently, Pence *et al.* (1978) have questioned criteria used in separating *C. felineus* from *C. subaequalis* (Molin, 1860). Kozlov (1977) did not list those species as occurring in the arctic fox in the USSR. *C. skriabini* Kozlov, Ovsiukova et Radkevich, 1963 has been reported from that host in Chukotka (Ovsiukova, 1967); it might also occur on SLI.

Both *C. felineus* and *C. subaequalis* are characteristic nematodes in felids. On the Alaskan mainland, we found *C. subaequalis* in 8 (13 %) of 55 lynx, *Felis lynx* (L.) (unpublished data). Kozlov (1977) indicated *C. subaequalis* has been reported in the USSR only from red foxes in Uzbekistan.

Crenosoma vulpis (Dujardin, 1844). *C. vulpis* was found in the lungs of 58 (4 %) of 1,390 foxes. It is the only species of the genus *Crenosoma* Molin, 1861 to be reported from canids in the USSR, where Ovsiukova (1967) found it in 11 % of 178 arctic foxes in Chukotka. In Iakutiia, only 1.2 % of 169 arctic foxes harbored that nematode (Gubanov, 1964).

Uncinaria stenocephala (Railliet, 1884). Hookworms

TABLE II. — *Summary of variation in infection rates between young of the year and adults and between sexes of foxes for the nine most common genera of helminths, with notation (*) of significant difference* ($p < 0.05$).

	Age class				*Sex*			
	Young		*Adult*		*Male*		*Female*	
Genus	*n*	%	*n*	%	*n*	%	*n*	%
Diphyllobothrium	1,090	3.4	159	0.6	729	3.0	824	2.3
Taenia	1,090	92.9	159	95.6	729	91.1	824	92.1
Echinococcus	1,090	82.1	159	58.5 *	729	74.2	824	79.4 *
Mesocestoides	1,090	1.5	159	1.2	729	1.6	824	1.1
Corynosoma	1,082	2.2	159	0.0	722	1.8	822	1.5
Trichinella	331	1.5	44	9.1 *	347	1.2	318	1.9
Toxascaris	1,090	86.7	159	69.8 *	729	83.9	824	84.8
Uncinaria	1,090	39.9	159	23.3 *	729	38.3	824	34.8
Crenosoma	910	3.8	149	8.0 *	627	5.4	737	3.2

occurred frequently in the foxes (overall prevalence 40 %) and in numbers from one to 40 per host ($\bar{x} \pm SD = 3.24 \pm 4.24$ in 298 foxes). The seasonal trend of occurrence appeared to be similar to that of *T. leonina,* with the highest prevalence in summer and autumn and lowest in winter.

The foxes probably became infected by ingestion of larvae around the dens, where the pups would appear to be most vulnerable. The larvae are highly cold-resistant (Balasingham, 1964). Their early-stage development is favored by warm soil-temperatures in summer (Gibbs and Gibbs, 1959).

The prevalence of *U. stenocephala* on the island was high, relative to records elsewhere. Ovsiukova (1967) found 26 % of 178 foxes infected in Chukotka, and Gubanov (1964) found it in only 4 % of 169 in Iakutiia. Only one (3 %) of 38 arctic foxes from northwestern Greenland harbored this nematode (Rausch *et al.,* 1983).

We analyzed our data for any evidence of influence of sex or age of the host on infection-rates and found that three out of the nine most abundant helminths occurred more often in the young foxes than in the adults, but the reverse was true for two others *(table II).* Our data tend to support the conclusion of Shiliaeva (1968), who pointed out that the young foxes apparently are more susceptible than adults to infection by many of the helminths, implying that a degree of immunity is acquired with age. For the few species that have great longevity, however, such as *Crenosoma vulpis* and *Trichinella nativa,* the proportion of foxes infected tends to increase with host-age.

The sex of the hosts appeared to have no consistent influence on infection-rate for the same nine genera of helminths. Although the observed difference between sexes in the case of *Echinococcus* tested as significant, that probably was an error of sampling, since it was not reflected in the rates for the other cestodes that would have been acquired by ingestion of arvicoline rodents.

DISCUSSION

Among the 22 species of helminths recorded from arctic foxes on the island, digeneans were poorly represented. Their relative scarcity might be attributable to at least three factors : 1) a low diversity of freshwater snails, of which we found only one species **, *Succinea strigata* Pfeiffer, generally common on wet tundra; 2) scarcity of certain marine invertebrates such as hermit crabs, *Pagurus* spp., because of the character of the island's shores; and 3) the small numbers of foxes examined during the warm months of the year, when trematodes might be more readily acquired.

Our findings on some of the other islands in the Bering Sea led us to expect several additional species of trematodes in foxes on SLI, but none of the following was recorded. *Microphallus pirum* (Afanas'ev, 1941), described from the arctic fox on the Commander Islands, has an extensive distribution in the North Pacific region; it was present in foxes on Amchitka Island (Aleutian Islands), and was abundant there in the sea otter, *Enhydra lutris* (Linnaeus) (Rausch, 1953 *b*). *Phocitrema fusiforme* Goto et Ozaki, 1930 was recorded by us from foxes on Amchitka and Kiska Islands, and from a spotted seal on SLI (VIII 50) (leg. ELS). *Cryptocotyle lingua* (Creplin, 1825) has an extensive range in the North Pacific region, but we have found it only once in an arctic fox in Alaska, at Hooper Bay (XII 58) (leg. FSLW). That trematode also occurred in six of 18 dogs at Kotzebue in November 1950 (Babero and Rausch, 1952). Still another, *Liliatrema skriabini* Gubanov, 1953, described from marine birds in the Kuril Islands,

** On 12 VI 90 one of us (RLR) found snails of another species, *Physella (Costatella) i. integra* (Haldeman, 1841), in a pond in wet tundra about 2 km west of Savoonga. The determination of the specimens was kindly provided by Dr T. J. Frest, Burke Memorial Washington State Museum, University of Washington.

might also be expected; we obtained it from an arctic fox and two pelagic cormorants on Amchitka Island (III 52) (Voucher specimens from arctic fox, USNM Helm. Coll. No. 81 323) and from one pelagic cormorant collected near Gambell, SLI (20 V 56) (leg. FHF) (Voucher specimen, USNM Helm. Coll. No. 81 322). *L. skriabini* has not been reported previously from the northern Bering Sea. Gubanov (1953) discovered the metacercarial stage in sculpins, *Myoxocephalus scorpius* (Linnaeus).

Freshwater snails serve as first intermediate host of two of the trematodes we recorded. As indicated by the finding of *Plagiorchis elegans* in a dog autopsied at Gambell, we judge that the cycle of that species must be completed on the island. The infection by *Alaria marcianae,* however, could only have involved a fox that had immigrated from the Alaskan mainland, since the second intermediate host, the wood frog, does not occur on SLI.

Among the cestodes recorded, *Taenia polyacantha, T. crassiceps* and *Echinococcus multilocularis* occur typically in foxes of the genera *Alopex* and *Vulpes* in the holarctic zone of tundra. Other canids sometimes become infected by these helminths (rarely by the *Taenia* spp.), but have little significance in the cycle under natural conditions. Foxes acquire these cestodes in the course of predation on arvicoline rodents, which serve as the intermediate hosts. Such rodents constitute their primary food-resource over most of their range in the Arctic, and the numerical density of the rodent populations strongly influences not only the population-dynamics of the foxes but the prevalence of the taeniids in them, as well (those interactions will be the subject of the next paper in this series).

Two of the species of cestodes, *Mesocestoides kirbyi* and *Diphyllobothrium dendriticum,* occur in numerous carnivorous and (in the case of *D. dendriticum*) piscivorous mammals and birds. The intermediate hosts of *D. dendriticum* are present on the island. If the cycle of *Mesocestoides* sp. is completed on SLI, however, the larval stage must be extremely rare. Hence, we suspect that most, if not all, of the foxes infected by that cestode were immigrants from the adjacent continents.

Of the acanthocephalans recorded, four species of the genus *Corynosoma (strumosum, semerme, validum,* and *villosum)* occur typically in pinnipeds, and we presume that the foxes become infected as do the pinnipeds, by feeding on marine fishes. The status of a fifth, *C. clavatum,* is uncertain, since it is known previously only from piscivorous birds in the Southern Hemisphere. The possibility exists that the taxon here designated *C. clavatum* represents a sibling species. Another species, *C. wegeneri* Heinze, 1934 (syn. *C. hadweni* Van Cleave, 1953) might also occur in arctic foxes on the island. We have two records of it there, one from a ringed seal in the vicinity of Gambell (IV 50) (leg. RLR) and the other from a ribbon seal near Savoonga in 1970 (leg. JJB). Also present in the intestine of the ribbon seal were *C. strumosum, C. semerme,* and *C. validum. Polymorphus* cf. *minutus,* recorded only once from the foxes of SLI, occurs typically in anseriform birds that feed on crustaceans and fishes. We recorded it elsewhere in Alaska only from a white-winged scoter, *Melanitta fusca* (Linnaeus).

The nematodes of the foxes included two species, *Cylicospirura felineus* and *Sobolophyme baturini,* which are characteristic helminths of felids and mustelids, respectively. *S. baturini* has not been recorded previously from the arctic fox but was described from a red fox taken near Cape Lopatka, southern Kamchatka (Petrov, 1930). *C. felineus* and *C. baturini,* as well as *Physaloptera* sp., were no doubt transported to SLI by their final hosts. The cycles of all other nematodes found in our sample, with the possible exception of *Crenosoma vulpis,* are completed on the island. *Trichinella nativa* probably is acquired by foxes from carrion, including that of marine mammals. Both *Uncinaria stenocephala* and *Toxascaris leonina* have direct cycles. Infective larvae of *T. leonina* encysted in paratenic hosts (northern voles), however, may be an additional source of infection for the foxes.

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