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JUNEAU, ALASKA

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SHEEP DISEASE REPORT

by
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Volume XIV
Project Progress Report
Federal Aid in Wildlife Restoration
Project W-17-5, Job 6.6R(2nd half) and Project W-17-6, Job 6.6R

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JOB PROGRESS REPORT (RESEARCH)

State: Alaska

Cooperators: Carol Neilsen and Kenneth A. Neiland

Project Nos.: W-17-5 and W-17-6 Project Title: Big Game Investigations

Job No.: 6.6R Job Title: Dall Sheep Disease and Parasites

Period Covered: January 1, 1973 - June 30, 1974

SUMMARY

In the first systematic study of the gastrointestinal nematodes of the Alaskan Dall sheep, a total of 79 animals were examined. Fifty-three sheep were collected on the Kenai Peninsula during 1970-1971, 18 sheep were collected at Dry Creek in the Alaska Range during 1972-1973, and the remaining 8 sheep were collected at various locations in Interior Alaska during 1964-1973.

Trichostrongylids (Nematoda: Trichostrongylidae) belonging to 5 genera and at least 11 species were the most frequently encountered and most abundant parasites. The species *Marshallagia marshalli, Ostertagia circumcincta, O. occidentalis, O. trifurcata, Nematodirus archari, N. davtiani, N. oiratianus*, and *N. spathiger* appear to be natural parasites of Dall sheep. In addition, several species were found which were probably acquired incidentally from other ungulates: *Ostertagia ostertagi, Teladorsagia davtiani* and *Nematodirella* spp. This is apparently the first report of *Nematodirella* spp. in wild *Ovis* in North America.

During the late winter lambs, in general, harbored more trichostrongylids than did adults. A classic "spring rise," or increase in trichostrongylid numbers, was seen in Dall sheep during April and May. As would be expected considering the ecological requirements of these genera, *Nematodirus* spp. became more abundant at first, then were followed later in the spring by *Ostertagia* spp.

Also encountered in the gastrointestinal tract were *Skrjabinema* spp. (Nematoda: Oxyuridae) and *Trichuris* spp. (Nematoda: Trichuridae). The former were sometimes found in large numbers, while the latter were frequent but not abundant.

The general effect of the gastrointestinal nematodes found is to chronically weaken their host, but usually only negligibly. Nevertheless, animals with moderate nematode burdens, particularly lambs during their first winter, are less able to digest crude proteins and dry matter due to the nematodes' pathological effects on the gastrointestinal mucosa. When coupled with loss of appetite another effect of the infection, reduction in digestibility, has serious consequences for animals on a low quality winter diet. The significance of these nematode infections to survival, population recruitment and range conditions is discussed.

CONTENTS

BACKGROUND

With increasing pressure on Alaskan Dall sheep (*Ovis dalli*) populations from land selection and development, increased hunting and recreation etc., it has become imperative to understand the factors which govern sheep population fluctuations if the species is to be properly managed. The debilitating effects of parasites and chronic diseases interact with, and may aggravate, the effects of decreasing range size, range deterioration, bad weather, deep snow, predation and overpopulation, thus leading to serious population declines.

The most serious and pathogenic parasites of domestic sheep (*Ovis aries*) are the gastrointestinal trichostrongylids (Levine 1968). These nematodes are worldwide in distribution and, as bloodsuckers, are chronically debilitating and even lethal to weakened adults and to lambs. A number of investigators (Appendix) have enumerated the qualitative trichostrongylid fauna of the bighorn sheep (*Ovis canadensis*) in North America but have been unable to quantify gastrointestinal burdens in sheep populations over a period of time. Thus the effects of trichostrongylids on wild sheep populations remain unknown.

There have been no systematic reports of either species identities or gastrointestinal helminth burdens in *Ovis dalli*. Over the past 12 years, however, the Alaska Department of Fish and Game has accumulated occasional Dall sheep parasite specimens, and in 1971, 1972, and 1973 staff biologists made three systematic collections of sheep in the course of physiology and population manipulation studies of this species. These collections provided an unusual opportunity to examine in detail for parasites the largest number, to our knowledge, of wild sheep ever accumulated. These sheep were taken during the winter, spring and summer months, and were a variety of ages. Not only was there abundant material for determining the particular helminth species infecting *Ovis dalli* in Alaska, but it was also possible to follow to some extent the dynamics of the gastrointestinal helminth population within the sheep. Comparisons of the dynamics, abundance, location and age "preferences" of different species could be made, and their varying effects on the host population began to become apparent. By examining the fecal pellets of sheep with known burdens, a basis can be established for future monitoring of these parasites in wild populations without the expense of sacrificing animals.

OBJECTIVES

To identify the species and determine the incidence and distribution of potential pathogens in Dall sheep.

To develop efficient techniques for recovering, identifying and estimating the populations of these potential pathogens.

To determine the extent to which these potential pathogens contribute to mortality or lower productivity of Dall sheep.

PROCEDURES

During 1973 gastrointestinal parasite specimens from a total of 79 Dall sheep were examined, counted and identified. Seventy-one of these sheep were taken in three major collections: 1970-1971 Kenai Peninsula, 1972 Dry Creek, and 1973 Dry Creek. Specimens from the remaining eight animals were accumulated from various locations in Interior Alaska between 1964 and 1973.

The 1970-1971 Kenai Peninsula collection began with the taking of five sheep on Surprise Mountain in April 1970 and continued with a series of 48 sheep collected on Crescent Mountain in November 1970 and January, February, March and April of 1971 (Nichols and Heimer 1972). Materials were recovered from them during 1971 (Neiland 1971b), but were not counted or identified until 1973.

Thirteen sheep were collected during the spring and early summer (March - July) of 1972 at Dry Creek (south of Fairbanks). Specimens from these sheep were recovered and counted during 1972 (Ericson and Neiland 1973), but were not identified to species until 1973.

Finally, five sheep were collected in early April 1973 at Dry Creek, and specimens were recovered, counted and identified (an additional five sheep were collected at the same time in the Granite Mountains, however materials from these sheep have not yet been examined).

All three major collections were made for scientific purposes. Departmental biologists Nichols, Heimer and their associates accumulated a variety of data on growth, reproduction and general biology from these sheep (Nichols and Smith 1971, Nichols and Heimer 1972, Heimer 1973). The gastrointestinal tracts and most of the major internal organs were then kindly made available for detailed parasitological examination. Ages of the sheep were determined by these biologists using the horn annuli method described by Geist (1966).

Of the eight sheep accumulated from miscellaneous locations, three were collected, two were found dead, two were killed by hunters, and one died after a month in captivity. A six-week-old lamb, found dead near Tok in 1973, was examined using the sieve technique, while parts of the gastrointestinal tracts of the remaining seven animals were superficially examined. Besides the animal from Tok, two sheep were from the Kenai Peninsula, two from the Granite Mountains, one from Chitina and one from Gulkana (all of these last three locations are in the southeastern Interior of the state). The animal which died in captivity was from Dry Creek.

Departmental records indicate that additional sheep have been collected or found dead over the past 12 years which did not yield gastrointestinal helminths when examined. It is suspected this was either due to incomplete examination under field conditions or to decomposition of the digestive tract, because all Dall sheep examined carefully during this study yielded helminths. The contents of the tract in a sheep are bulky and voluminous, and the small helminths inhabiting this area are easily overlooked.

The 79 Dall sheep from which trichostrongylids, pinworms or whipworms were recovered were unfortunately not examined with uniform throughness and method, and quantitative comparisons should not be made between some animals. The five 1970 Surprise Mountain (Kenai) sheep were examined quickly under field conditions, therefore it is likely that many specimens were overlooked. The 53 Kenai Peninsula sheep collected in 1970-1971 were examined carefully by experienced personnel, but due to the time constraints a variety of methods were utilized: sometimes trichostrongylids were taken only until 50 males were recovered, sometimes a sample of specimens was taken and the total nematodes seen "estimated," and sometimes all the specimens seen were recovered. Unfortunately, no records were kept of which procedures were used for which sheep, therefore, the actual quantities of trichostrongylids obtained from the Kenai sheep should be viewed with a measure of doubt.

The sieve procedure for rapid recovery of small helminths from the Dall sheep gastrointestinal tract posterior to the omasum has been described previously (Ericson and Neiland 1973). This procedure was employed for examining 7 of the 13, 1972 Dry Creek sheep and all 5 of the 1973 Dry Creek sheep. For four of the five 1973 Dry Creek sheep, however, only 20 percent of the tract contents were examined; the total parasite burden was estimated by multiplying the findings by five (the remaining unexamined 80 percent was preserved and stored.) This 20 percent sampling procedure was adopted to reduce the time required to examine one sheep gastrointestinal tract and identify the specimens found from approximately 15 days to 4 days. Soulsby (1965) recommends at least a 10 percent sample for arriving at an accurate estimate of total burden, and most other investigators examining several or more sheep have utilized sampling (Allen 1955, Becklund and Senger 1967, Uhazy and Holmes 1971).

For three of the 1970-1971 Kenai Peninsula sheep, the anterior digestive tract was not available for necropsy, although the caecum was available. Since trichostrongylids are primarily inhabitants of the digestive tract from the abomasum through the ileum, and pinworms and whipworms inhabit the caecum and colon, it follows that 53 of these sheep were examined for pinworms and whipworms but only 50 were examined for trichostrongylids.

All pinworm and whipworm specimens were identified to genus, and all trichostrongylid specimens were identified to species. With experience, it became possible to identify the following common specimens using the dissecting microscope only: *Marshallagia marshalli* (Ransom 1907) Orloff 1933, *Ostertagia circumcincta* (Stadelmann 1894) Ransom 1907, *Ostertagia occidentalis* Ransom 1907, *Nematodirus archari* Sokolova 1948, *Nematodirus davtiani* Grigorian 1949, *Nematodirus spathiger* (Railliet 1896) Railliet and Henry 1909, *Nematodirella* Yorke and Maplestone 1926, *Skrjabinema* Vereshchagin 1926, and *Trichuris* Roederev 1761. A Zeiss Standard GFL compound microscope was employed to distinguish the species *Ostertagia ostertagi* (Stiles 1892) Ransom 1907, *Ostertagia trifurcata* Ransom 1907, *Teladorsagia davtiani* Andreeva and Satubaldin 1954 and *Nematodirus oiratianus* Rajewskaya 1929 as well as to identify specimens of the previous group of species which could not clearly be seen with the dissecting microscope. Female and immature trichostrongylids were not identified to species.

The 50 Kenai Peninsula trichostrongylid specimen sets and the 13 Dry Creek trichostrongylid sets from 1972 were preserved in an alcohol-acetic acid-formalin-glycerin solution, while the 5 trichostrongylid specimen sets from the 1973 Dry Creek sheep were preserved in a 70 percent alcohol-glycerine mixture. Specimens examined under the compound microscope were temporarily mounted in 70 percent alcohol-glycerine.

The gastrointestinal tracts of seven of the eight "miscellaneous location" sheep were divided into the abomasum and the first several feet of the small intestine for examination. The caecum was also examined for two of these seven sheep. The eighth animal's tract was divided for examination into the abomasum, duodenum, anterior and posterior small intestine, caecum, and colon.

For the fifty 1970-1971 Kenai Peninsula sheep, the gastrointestinal tract was divided into the abomasum, small intestine (including the duodenum) and caecum, and the trichostrongylids recovered were associated with one of these three locations. The gastrointestinal tracts of the thirteen 1972 Dry Creek sheep were divided into the abomasum, duodenum (i.e. approximately the first 250 cm of small intestine beyond the pyloric sphincter), anterior half of the (remaining) small intestine, posterior half of the small intestine, caecum and colon. The recovered trichostrongylids were then from one of these six locations. Two of the five 1973 Dry Creek sheep tracts were similarly divided into these six areas. However, as it became obvious that a number of *Nematodirus* species were located together in the anterior part of the small intestine just below the duodenum, the anterior small intestine was analyzed in smaller subunits. The anterior half of the small intestine of one of the 1973 Dry Creek sheep was divided in half, the part immediately behind the duodenum being designated "anterior small intestine A" and the part nearest the middle of the intestine as "anterior small intestine B" or "jejunum;" the other parts of the digestive tract were divided as in the previous sheep, giving a total of seven locations. Finally, for the remaining two sheep (of the five taken in 1973 at Dry Creek), "anterior small intestine A" was divided into four equal parts of one meter length, the part nearest the duodenum designated "AS1," the next "AS2," then "AS3" and "AS4" nearest the jejunum. In addition, the abomasum was divided into a fundic portion (including the cardiac area and the fundus) and a pyloric portion. These further subdivisions led to a total of 12 locations. In one of these two sheep "AS1" was again divided in half, with "AS1.18" nearest the duodenum and "AS1.36" nearest "AS2," yielding a total of 13 gastrointestinal locations (see Fig. 1). The entire small intestine of an adult Dall sheep is approximately 85 meters long.

A large majority of the animals examined, particularly those older than three years of age, were ewes. Therefore, a major assumption of the study was that the parasitological findings for these collections were representative of the sheep populations as a whole. Because of certain phenomena such as the "spring rise," to be discussed below, this assumption is not entirely valid. However, it was useful in determining the general picture of the dynamics of the gastrointestinal helminth burden within the sheep population.

FINDINGS

A. Trichostrongylids

Trichostrongylids or "stomach worms" are small nematodes of the family Trichostrongylidae Leiper, 1912. They were the most frequent and most abundant parasite encountered in the Dall sheep gastrointestinal tract. All sheep carefully examined harbored trichostrongylids, including a six-week-old lamb, which had one egg-filled female trichostrongylid in its caecum.

1. Total Number of Trichostrongylids

The groups of sheep from different localities tended to have different numbers of trichostrongylids, however this was probably an artifact resulting from the unrecorded methods used to recover specimens from the

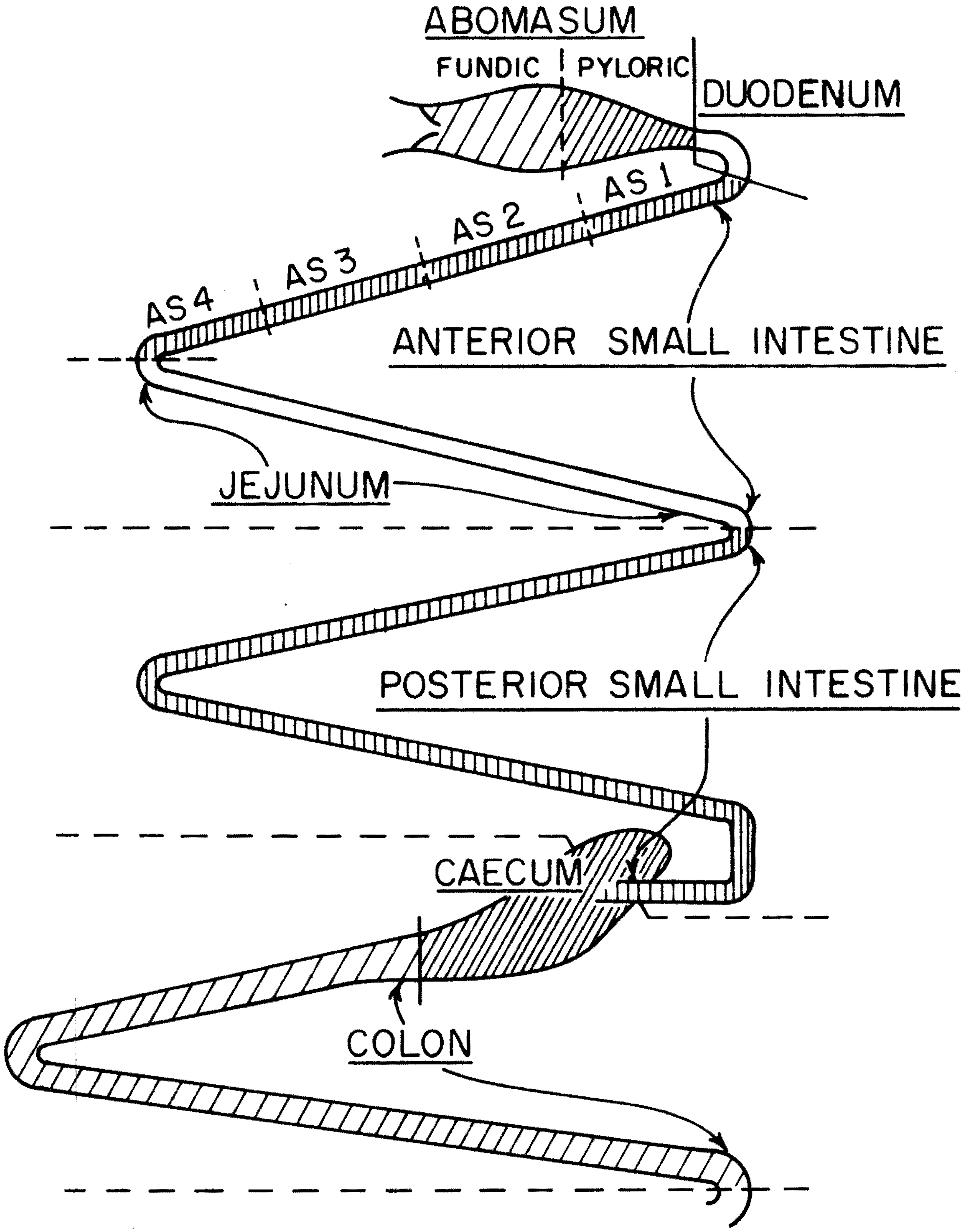


Fig. 1. Diagrammatic representation (not strictly to scale) of the Dall sheep gastrointestinal tract, divided into sections for helminthological examination.

50 Kenai Peninsula sheep and from the 8 sheep from various localities. Numbers of trichostrongylids in the Kenai sheep ranged from 2 to 1,910 mature specimens (Tables 1 and 2), and numbers in the 8 sheep from miscellaneous localities ranged from 1 to 305 (Table 3). Both of these ranges are certainly lower than those of the 1972 Dry Creek sheep (125 to 4,165 mature specimens, Table II in Ericson and Neiland 1973), and the 1973 Dry Creek sheep (1,400 to 6,725 mature specimens, Table 4), as would be expected because of the more intensive specimen recovery effort expended on the Dry Creek sheep. Thus it is not possible to compare the Kenai and Dry Creek sheep groups on the basis of numbers of trichostrongylids.

Because of uniform methods, however, the 1972 and 1973 Dry Creek materials may be compared if we assume that adequate numbers of animals were examined. Ten spring 1972 Dry Creek burdens averaged 1,360 mature trichostrongylids per animal while 5 spring 1973 burdens (Table 4) averaged 3,450 mature trichostrongylids per animal. However, it is unwise to compare trichostrongylid burdens (particularly "average burdens") on the basis of numbers alone because the actual number of worms which constitutes a threat to wild sheep depends on a variety of factors: the age, size, weight, general health and nutritional condition of the host, the duration of the infection, and the age and species of trichostrongylids present. "Danger threshold" numbers established for domestic sheep have little relevence to wild sheep because, unlike domestic animals, wild sheep are not crowded into artificial groupings but rather undergo daily stresses of weather, food finding and predators.

In general the greatest numbers of mature trichostrongylids were found in the abomasum, duodenum and the anterior two meters (1/8) of the small intestine. The number of immature trichostrongylids differed widely, partly because it is very difficult to detect, recover and estimate the numbers of immature trichostrongylids, and partly because the number present varies greatly with the season of the year (see section 6).

2. Species of Trichostrongylids and their Locations in the Host

Trichostrongylid specimens examined from 76 Dall sheep belonged to 5 genera and at least 11 species (only part of the gastrointestinal tract, the posterior small intestine, was available for necropsy of one 1972 Dry Creek sheep, #3575, so this individual has been omitted from the discussion). In mixed infections it is generally impossible to identify female trichostrongylids to species, therefore, only male specimens were examined and identified. Table 5 shows the prevalences and intensities of the different trichostrongylid species for all 75 sheep examined, and Tables 6, 7, 8, and 9 show similar information for each group of sheep.

(a) *Marshallagia marshalli* Ransom, 1907

Marshallagia marshalli was the most frequently encountered (96%) and most generally abundant trichostrongylid ($\bar{x} = 151$). A total of 2,027

Table 1. Number of trichostrongylids, 1970 Surprise Mountain, Kenai Peninsula.

					Abomasum				Small Intestine				Total, G.I. Tract			
No.	Autopsy No.	Month Taken	Sex	Age Yrs	M	F	Total Mature	Im.	M	F	Total Mature	Im.	M	F	Total Mature	Im.
1	2735	Apr.	F	7	35	70	105	-	1	-	1	-	35	70	105	-
2	2736	Apr.	F	2	15	140	150	-	2	1	3	-	15	140	155	-
3	2737	Apr.	F	10	9	60	70	10	-	-	-	-	9	60	70	10
4	2738	Apr.	F	2	2	5	7	1	3	2	5	-	5	7	12	11

Table 2. Number of trichostrongylids, 1970-1971 Crescent Mountain, Kenai Peninsula.

					Abomasum				Small Intestine				Total, G.I. Tract			
No.	Autopsy No.	Month Taken	Sex	Age Yrs	M	F	Total Mature	Im.	M	F	Total Mature	Im.	M	F	Total Mature	Im.
1	3244	Nov.	M	.5	–	6	6	–	20	33	53	–	20	39	59	–
2	3250	Nov.	M	.5	5	25	30	–	–	–	–	–	5	25	30	–
3	3252	Nov.	M	.5	2	10	12	–	2	2	4	–	4	12	16	–
4	3247	Nov.	F	2.5	9	12	21	–	–	–	–	–	9	12	21	–
5	3253	Nov.	F	2.5	54	10	64	–	51	5	56	–	105	15	120	–
6	3251	Nov.	F	3.5	7	27	34	–	–	–	–	–	7	27	34	–
7	3237	Nov.	F	6.5	4	1	5	–	–	–	–	–	4	1	5	–
8	3241	Nov.	F	7.5	2	–	2	–	–	–	–	–	2	–	2	–
9	3243	Nov.	F	8.5	8	18	26	–	1	1	2	–	9	19	28	–
10	3255	Jan.	M	.5	57	9	63	–	19	5	24	–	76	14	90	–
11	3262	Jan.	F	.5	14	5	19	–	4	–	4	–	18	5	23	–
12	3259	Jan.	F	1.5	10	1	11	–	28	3	31	–	38	4	42	–
13	3273	Jan.	F	1.5	24	4	28	–	15	3	18	–	39	7	46	–
14	3269	Jan.	F	3.5	33	8	41	–	6	4	10	–	39	12	51	–
15	3270	Jan.	F	6.5	23	13	36	–	5	4	9	–	28	17	45	–
16	3267	Jan.	F	8.5	51	9	60	–	27	7	34	–	78	16	94	–
17	3236	Feb.	M	1.75	8	–	8	–	–	–	–	–	8	–	8	–
18	3275	Feb.	F	1.75	1	–	1	–	1	–	1	–	2	–	2	–
19	3235	Feb.	F	2.75	6	1	7	–	42	14	56	10	48	15	63	10
20	3239	Feb.	F	2.75	308	310	618	25	–	–	–	–	308	310	618	25
21	3268	Feb.	M	2.75	23	32	55	–	small int. missing				23	32	55	–
22	3249	Feb.	M	3.75	74	69	143	–	5	6	11	–	79	75	154	–
23	3261	Feb.	F	6.75	4	5	9	–	1	1	2	–	5	6	11	–
24	3234	Feb.	F	9.5	125	162	287	20	13	11	24	–	138	173	311	20
25	3276	Feb.	F	13.5	46	10	56	1	–	–	–	–	46	10	56	1
26	3256	Mar.	F	.75	109	205	314	–	70	112	182	–	179	317	496	–
27	3263	Mar.	M	.75	322	539	861	20	25	18	43	–	347	557	904	20
28	3271	Mar.	M	.75	594	727	1321	20	247	342	589	–	841	1069	1910	20
29	3264	Mar.	M	1.75	53	4	57	–	25	12	37	–	78	16	94	–
30	3272	Mar.	F	1.75	28	3	31	–	43	4	47	–	71	7	78	–
31	3274	Mar.	F	1.75	17	94	111	–	27	57	84	–	44	151	195	–
32	3277	Mar.	M	1.75	250	317	567	5	3	6	9	–	253	323	576	5

Table 2. Continued.

					Abomasum				Small Intestine				Total, G.I. Tract			
No.	Autopsy No.	Month Taken	Sex	Age Yrs	M	F	Total Mature	Im.	M	F	Total Mature	Im.	M	F	Total Mature	Im.
33	3266	Mar.	F	3.75	179	263	442	-	-	-	-	-	179	263	442	-
34	3258	Mar.	F	5.75	77	128	205	-	78	163	241	-	155	291	446	-
35	3257	Mar.	F	7+	83	193	276	-	-	-	-	-	83	193	276	-
36	3265	Mar.	F	9.75	6	17	23	-	-	-	-	-	6	17	23	-
37	3254	Mar.	F	10.75	54	4	58	-	39	7	46	-	93	11	104	-
38	3331	Apr.	F	1	Abomasum missing				91	71	162	-	91	71	162	-
39	3332	Apr.	M	1	46	73	119	-	30	52	82	-	76	125	201	-
40	3242	Apr.	F	1	36	51	87	-	165	220	385	5	201	271	472	5
41	3240	Apr.	M	2	44	-	44	-	8	-	8	-	52	-	52	-
42	3248	Apr.	M	2	110	172	282	10	1	-	1	-	111	172	283	10
43	3330	Apr.	F	5	-	-	-	-	42	4	46	-	42	4	46	-
44	3245	Apr.	F	5	54	59	113	3	3	-	3	-	57	59	116	3
45	3238	Apr.	F	6	46	6	52	-	25	1	26	-	71	7	78	-
46	3333	Apr.	F	12	9	6	15	-	-	2	2	-	9	8	17	-

Table 3. Number of trichostrongylids, 1964-1973 sheep from miscellaneous locations.

					Abomasum				Duodenum				Small Intestine Caecum and Colon				Total, G.I. Tract			
No.	Autopsy No.	Month Taken	Sex	Age Yrs.	M	F	Total Mature	Im.	M	F	Total Mature	Im.	M	F	Total Mature	Im.	M	F	Total Mature	Im.
1	3910	July	F	6 wks.	-	-	-	-	-	-	-	-	-	1	1	-	-	1	1	-
2	2576	July	F	3	3	4	7	-	-	-	-	-	-	-	-	-	3	4	7	-
3	7002	Sept.	M	3	75	230	305	-	-	-	-	-	-	-	-	-	75	230	305	-
4	3334	Aug.	F	6	40	48	88	-	-	-	-	-	-	-	-	-	40	48	88	-
5	3170	May	M	9	1	6	7	-	-	-	-	-	-	-	-	-	1	6	7	-
6	2037	Sept.	F	9+	1	8	9	-	-	-	-	-	-	-	-	-	1	8	9	-
7	3338	Aug.	M	9+	3	8	11	-	-	-	-	-	1	1	2	-	4	9	13	-
8	3339	Aug.	M	10	51	231	282	-	-	-	-	-	-	-	-	-	51	231	282	-

Table 4. Number of trichostrongylids, 1973 Dry Creek sheep (*estimated by 20% sample).

					Abomasum				Duodenum				Small Intestine Caecum and Colon				Total, G.I. Tract			
No.	Autopsy No.	Month Taken	Sex	Age Yrs.	M	F	Total Mature	Im.	M	F	Total Mature	Im.	M	F	Total Mature	Im.	M	F	Total Mature	Im.
1	3893*	Apr.	F	8	565	955	1420	60	65	25	90	105	740	410	1150	805	1370	1390	2760	970
2	3894*	Apr.	F	2	470	715	1185	225	175	90	270	145	1605	850	2460	2205	2250	1660	3910	2575
3	3895*	Apr.	F	7	570	825	1390	375	35	5	40	160	745	280	1025	24,220	1345	1110	2455	24,755
4	3896	Apr.	F	8	2045	2745	4790	100	205	180	385	1400	950	600	1550	12,550	3200	3525	6725	14,335
5	3897*	Apr.	F	5	210	425	635	235	5	-	5	125	675	85	760	905	890	510	1400	1265

Table 5. Prevalence and intensity of trichostrongylids, all 1964-1973 *Ovis dalli*.

	Ovis dalli			Intensity		
	No. Examined	No. Infected	Prevalence %	$\bar{x}$	Range	Total Specimens
Males:						
Marshallagia marshalli	74*	71	96	151	1-2027	10,724
Ostertagia circumcincta	74	9	12	96	1-602	868
O. occidentalis	74	27	37	10	1-52	272
O. ostertagi	74	2	3	12	2-22	24
O. trifurcata	74	8	11	18	1-79	145
all *Ostertagia* spp.	74	29	39	45	1-734	1309
Teladorsagia davtiani	74	7	10	9	1-28	63
Nematodirus archari	75	44	59	109	1-1180	4814
N. davtiani	75	47	63	16	1-214	769
N. oiratianus	75	36	48	19	1-110	681
N. spathiger	75	30	40	69	1-431	2063
N. male spp. unidentified						6
all *Nematodirus* spp.	75	47	63	177	1-1839	8333
Nematodirella spp.	75	2	3	64	7-121	128
Females:						
Marshallagia, Ostertagia, Teladorsagia, Nematodirus and *Nematodirella* spp.	75	71	95	309	1-3525	21,911
Total Males	75	74	99	278	1-3199	20,557
Total mature trichostrongylids	75	75	100	566	1-6724	42,468

* For one sheep (#3331) the abomasum was not available for necropsy.

Table 6. 1970-1971 Kenai Peninsula sheep: prevalence and intensity of trichostrongylids.

	Ovis dalli No. Examined	No. Infected	Prevalence %	Intensity $\bar{x}$	Range	Total Specimens
Males:						
Marshallagia marshalli	49*	47	96	64	1-579	3004
Ostertagia circumcincta	49	1	2	1	(1)	1
O. occidentalis	49	9	18	3	1-12	24
O. ostertagi	49	-	-	-	-	-
O. trifurcata	49	-	-	-	-	-
all *Ostertagia* spp.	49	10	20	3	1-12	25
Teladorsagia davtiani	49	-	-	-	-	-
Nematodirus archari	50	29	58	13	1-74	364
N. davtiani	50	24	48	9	1-43	209
N. oiratianus	50	23	46	18	1-67	402
N. spathiger	50	19	38	12	1-97	236
N. spp. unidentified	50	1	2	(1)	-	1
Nematodirus spp.	50	40	80	30	1-250	1212
all *Nematodirella* spp.	-	-	-	-	-	-
Females (all species)	50	46	92	110	1-1069	5053
Total Males	50	50	100	85	2-841	4241
Total mature trichostrongylids	50	50	100	186	2-1910	9294

* #3331: Abomasum missing

Table 7. 1972 Dry Creek sheep: prevalence and intensity of trichostrongylids.

	Ovis dalli No. Examined	No. Infected	Prevalence %	Intensity $\bar{x}$	Range	Total Specimens
Males:						
Marshallagia marshalli	12	12	100	317	77-762	3808
Ostertagia circumcincta	12	8	67	108	1-602	867
O. occidentalis	12	12	100	16	1-52	197
O. ostertagi	12	1	8	(22)	-	22
O. trifurcata	12	7	58	20	3-79	144
all *Ostertagia* spp.	12	12	100	103	1-734	1230
Teladorsagia davtiani	12	7	58	9	1-28	63
Nematodirus archari	12	10	83	137	4-775	1365
N. davtiani	12	8	67	11	1-32	88
N. oiratianus	12	9	75	25	1-110	227
N. spathiger	12	5	42	59	2-202	294*
N. spp. unidentified	12	3	25	-	-	5
all *Nematodirus* spp.	12	11	92	180	18-1180	1979
Nematodirella spp.	12	-	-	-	-	-
Total females	12	12	100	678	90-2270	8130
Total males	12	12	100	590	39-1656	7080
Total mature trichostrongylids	12	12	100	1268	129-3928	15,210

* #3575, which has been omitted here because only part of its gastrointestinal tract was available for necropsy, contained 10 *N. spathiger*.

Table 8. 1973 Dry Creek sheep: prevalence and intensity of trichostrongylids.

	Ovis dalli					
	No. Examined	No. Infected	Prevalence %	Intensity $\bar{x}$	Intensity Range	Total Specimens
Males:						
Marshallagia marshalli	5	5	100	749	210-2027	3750
Ostertagia circumcincta	5	-	-	-	-	-
O. occidentalis	5	3	60	14	5-22	42
O. ostertagi	5	-	-	-	-	-
O. trifurcata	5	-	-	-	-	-
all *Ostertagia* spp.	5	3	60	14	5-22	42
Nematodirus archari	5	5	100	617	155-1180	3085
N. davtiani	5	5	100	94	2-214	472
N. oiratianus	5	3	60	17	5-35	51
N. spathiger	5	5	100	307	85-431	1533
all *Nematodirus* spp.	5	5	100	1038	681-1839	5141
Nematodirella spp.	5	2	40	64	7-121	128
Total females	5	5	100	1658	510-3525	8190
Total males	5	5	100	1812	892-3199	9061
Total mature trichostrongylids	5	5	100	3450	1402-6724	17,251

Table 9. 1964-1973 miscellaneous locations.

	Ovis dalli No. Examined	No. Infected	Prevalence %	Intensity $\bar{x}$	Range	Total Specimens
Males:						
Marshallagia marshalli	8	7	88	23	1-74	162
Ostertagia circumcincta	8	-	-		-	-
O. occidentalis	8	3	38	3	1-7	9
O. ostertagi	8	1	13	(2)	-	2
O. trifurcata	8	1	13	(1)	-	1
all *Ostertagia* spp.	8	4	50	3	1-9	12
Teladorsagia davtiani	8	-	-	-	-	-
Nematodirus archari	8	-	-	-	-	-
N. davtiani	8	-	-	-	-	-
N. oiratianus	8	1	13	(1)	-	1
N. spathiger	8	-	-	-	-	-
all *Nematodirus* spp.	8	1	13	(1)	-	1
Nematodirella spp.	8	-	-	-	-	-
Total females	8	8	100	67	1-231	538
Total males	8	7	88	25	1-75	175
Total mature trichostrongylids	8	8	100	89	1-306	713

M. marshalli males in an 8-year-old ewe taken at Dry Creek in 1973 constituted the most male specimens of any single species seen in Dall sheep. When all specimens were carefully recovered and counted, as they were for the seventeen 1972 and 1973 Dry Creek sheep, the average was 445 mature male *M. marshalli* per sheep. *M. marshalli* is a parasite of the abomasum, occurring both in the fundic and pyloric portions of that organ. It is occasionally seen in the lower digestive tract (Table 10): 5 percent (515/10,724) of the total *M. marshalli* found were located beyond the abomasum. Where duodenum records were kept separately, 57 percent (277/486) of the *M. marshalli* males in the lower digestive tract were located in the duodenum while the remainder were located elsewhere. For the 23 sheep harboring *M. marshalli* elsewhere than the abomasum, the average number seen was 22 specimens (515/23). However, nearly 50 percent (253/515) of the extra-abomasal *M. marshalli* were found in one sheep, a 7-year-old ewe from Dry Creek taken on May 5, 1972 and carrying a fetus two weeks from full term. The large numbers of *M. marshalli* seen in the lower digestive tract of this ewe can be ascribed to the "spring rise" phenomenon, to be discussed later, during which trichostrongylids are purged out of the tract.

(b) *Ostertagia* Ransom, 1907

Ostertagia is a genus common in the abomasum of domestic sheep. The genus was seen in 39 percent of the Dall sheep examined, but in most cases the infections consisted of less than 50 mature male specimens. *Ostertagia occidentalis* Ransom, 1907 was the most prevalent species, as it was seen in 27 of 74 sheep examined: 12 of 56 sheep from the Kenai Peninsula and miscellaneous locations and 15 of 17 from 1972 and 1973 Dry Creek sheep. The largest *O. occidentalis* infection in any one animal was 52 mature males; the average infection was only 10 males. In 24 of the 27 animals in which it was found, *O. occidentalis* was located in the abomasum. Only four percent (12/272) of the mature *O. occidentalis* males found were in the duodenum or anterior small intestine of the three remaining sheep; these three sheep all had, in addition, moderate *O. occidentalis* infections in their abomasa. *O. occidentalis* was found in 10 of 29 sheep taken between late April and September, and in 14 of 45 sheep taken between November and early April.

Ostertagia circumcincta (Stadelmann 1894) Ransom, 1907 was the next most prevalent species of the genus: it was seen in 9 of the 74 sheep examined. However, the largest *O. circumcincta* infection in any one animal, 602 mature males, was by far the largest infection seen for this genus and was third after *N. archari* and *M. marshalli* in the total number of mature males seen of any one species. One of 49 sheep from the Kenai Peninsula, 8 of 12 sheep from Dry Creek in 1972, none of the 5 sheep from Dry Creek in 1973, and none of the 8 sheep from miscellaneous locations harbored *O. circumcincta*. Of the total mature male *O. circumcincta* found, 94 percent (811/868) were located in the abomasum, 5 percent (46/868) in the duodenum and 1 percent (11/868) in the anterior half of the small intestine. All sheep which harbored *O. circumcincta* in their duodenum or small intestine had specimens in the abomasum. All of the *O. circumcincta* found were in 9 of the 29 sheep taken between late April and September; none were found in the 45 sheep taken between November and early April.

Table 10. Extra-abomasal *Marshallagia marshalli* (mature males).

Sheep No.	Collection Date	Location	Sex	Age Yrs.	Mature Male *M. marshalli* Duodenum	Lower Digestive Tract	Small Intestine (undivided)
3578	5/5/72	Dry Cr.	F	4	42	8	
3579	5/5/72	Dry Cr.	F	7	13	6	
3580	5/5/72	Dry Cr.	F	7	143	110	
3581	5/4/72	Dry Cr.	F	1	-	1	
3623	6/5/72	Dry Cr.	F	1	1	-	
3624	6/5/72	Dry Cr.	F	13	10	-	
3695	7/9/72	Dry Cr.	M	1	63	-	
3697	7/9/72	Dry Cr.	F	4	1	1	
3870	11/17/72	Dry Cr.	F	5	-	1	
3894	4/10/73	Dry Cr.	F	2	1	-	
3895	4/10/73	Dry Cr.	F	7	-	10	
3896	4/10/73	Dry Cr.	F	8	3	2	
3897	4/10/73	Dry Cr.	F	5	-	70	
				Total	277	209	
3234	2/26/71	Kenai Pen.	F	9.5			1
3235	2/26/71	Kenai Pen.	F	2.5			1
3238	4/27/71	Kenai Pen.	F	6			2
3242	4/27/71	Kenai Pen.	F	1			2
3249	2/26/71	Kenai Pen.	M	3.75			1
3254	3/18/71	Kenai Pen.	F	10.75			2
3259	1/14/71	Kenai Pen.	M	1.5			2
3270	1/14/71	Kenai Pen.	F	6.5			2
3273	1/14/71	Kenai Pen.	M	1.5			14
3277	3/18/71	Kenai Pen.	M	1.75			2
						Total	29

Total extra-abomasal *M. marshalli*

Dry Creek (duodenum)	- 277
Dry Creek (lower tract)	- 209
Dry Creek	486
Kenai (small intestine)	- 29
Total All	515

Ostertagia trifurcata Ransom, 1907 was a less common species. It was found in 8 of the 74 sheep: 6 of 8 sheep from the 1972 Dry Creek collection, one from a Dry Creek animal held a month in captivity and one from the Kenai Peninsula. The largest number of male *O. trifurcata* in one infection was 79. The average burden was only 18 specimens. Of the total mature male *O. trifurcata*, 89 percent (129/145) were found in the abomasum, 8 percent (12/145) in the duodenum, and 3 percent (4/145) in the small intestine. All sheep with *O. trifurcata* in the duodenum or intestine had at least some of the species also in the abomasum. *O. trifurcata* was found in 8 of the 29 sheep taken between late April and September, but in none of the 45 sheep taken between November and early April.

Ostertagia ostertagi (Stiles 1892) Ransom, 1907 was seen in only 2 of the 74 sheep examined: 2 mature males were found in the abomasum of a ram taken in August 1971 from the Granite Mountains, and 22 males were found in the abomasum of a ewe taken from Dry Creek in July 1972.

In general, all four species of *Ostertagia* encountered were primarily of abomasal origin, with only occasional specimens in the duodenum and anterior small intestine. The species *O. circumcincta* and *O. trifurcata* seem to occur primarily in the spring and summer months, while *O. occidentalis* was found year-round although perhaps slightly more prevalent in the spring and summer.

(c) *Teladorsagia davtiani* Andreeva and Saturbaldin, 1954

The monotypic genus *Teladorsagia* was encountered in 7 of the 74 sheep examined. All 7 sheep belonged to the 1972 Dry Creek collection. The largest number of mature male *T. davtiani* was 28. Of the total mature male *T. davtiani*, 87 percent (55/63) were found in the abomasum, 8 percent (5/63) in the duodenum and 5 percent (3/63) in the anterior small intestine. All sheep with *T. davtiani* in the duodenum and small intestine had a number in the abomasum too. All seven sheep harboring *T. davtiani* were collected in May, June and July. However, there were more specimens present in June and July: the two sheep taken in May averaged 1.5 *T. davtiani* per animal, while the two taken in June and the three taken in July averaged 12 per animal.

(d) *Nematodirus* Ransom, 1907

Nematodirus archari Sokolova, 1948 was the second most abundant trichostrongylid found after *Marshallagia marshalli*. The total of 1,180 mature male *N. archari* in a 2-year-old ewe taken April 10, 1973 at Dry Creek constituted the second most male specimens of any single trichostrongylid species seen in a Dall sheep. The members of the genus *Nematodirus* are primarily parasites of the upper small intestine. Subdivision of the anterior small intestine into units (as described in Procedures) revealed that the individual species of *Nematodirus* are somewhat geographically separated. In the 1970-71 Kenai Peninsula sheep, which were analyzed on the basis of the abomasum and entire small intestine, 7 percent (26/364) of the total mature male *N. archari* were found in the abomasum of the 29 sheep harboring the species (Table 11). The remaining 93 percent (338/364) were found in the small intestine.

Table 11. 1964-1971 Kenai Peninsula sheep: location of *N. archari*.

Sheep No.	Abomasum	Small Intestine
2735	2	1
3234	10	4
3235	-	11
3238	1	13
3240	1	8
3242	2	35
3244	-	1
3245	-	3
3247	1	-
3248	1	1
3249	2	-
3253	-	15
3254	-	35
3256	-	15
3257	2	-
3258	-	20
3259	1	1
3261	1	-
3263	-	3
3264	-	12
3267	-	22
3270	-	3
3271	1	73
3272	-	5
3274	-	4
3330	-	7
3331	missing	39
3332	-	7
3333	1	-
Total	26	338

In the 15 sheep taken in 1972 and 1973 from Dry Creek which did contain *N. archari* (Table 12), 5 percent (223/4450) of the total mature males were found in the abomasum, 13 percent (597/4450) in the duodenum, 70 percent (3118/4450) in the anterior half of the small intestine, 4 percent (179/4450) in the posterior half of the small intestine, and 8 percent (333/4450) in the caecum and colon. When the anterior small intestine was subdivided in half in three sheep, the anterior half (anterior small intestine A) contained 77 percent (1660/2170) of the total mature male *N. archari* found in these sheep, while the posterior half ("jejunum") contained only 1 percent (21/2170) of the total. When in 2 sheep "anterior small intestine A" was subdivided into 4 one-meter sections, AS1 contained 54 percent (780/1455) of the total mature male *N. archari* AS2 contained 15 percent (215/1455), AS3 contained 14 percent (205/1455), and AS4 contained 8 percent (110/1455). This indicates that the duodenum and first 3 meters of the small intestine contain about 96 percent of the mature *N. archari*.

The other species of *Nematodirus* were less abundant than *N. archari*, but one species, *N. davtiani* Grigorian, 1949, was more prevalent (Table 5), although the numbers of mature male *N. davtiani* did not exceed 214 specimens in any of the 47 sheep in which it occurred. Among 24 of 50 sheep from the Kenai which harbored *N. davtiani*, 11 of the 23 from which abomasa were available harbored the species in this organ (Table 13). At the same time this nematode was found in the small intestine of 20 of 24 of the sheep, and in both organs in 7 of 23 sheep. Of the total mature *N. davtiani* males, 22 percent (46/209) occurred in the abomasum while 78 percent (163/209) occurred in the entire small intestine. Thirteen of the 17 sheep taken in 1972 and 1973 in Dry Creek harbored *N. davtiani*, 7 in the abomasum, 12 in the duodenum, 10 in the anterior small intestine, 3 in the posterior small intestine, and 2 in the colon (Table 14). Twenty-one percent (117/560) of the total mature males were found in the abomasum, 55 percent (309/560 were found in the duodenum, 12 percent (67/560) in the anterior half of the small intestine, 3 percent (16/560) in the posterior small intestine, and 9 percent (51/560) in the caecum or colon. When the abomasum and anterior small intestine were subdivided in two sheep, all *N. davtiani* present were found in the pyloric part of the abomasum, in the duodenum, and in the first following meter of the small intestine. Thus it appears that the pyloric portion of the abomasum, the duodenum and the first meter of the small intestine may contain about 88 percent of the mature *N. davtiani*.

The next most prevalent species of *Nematodirus* after *N. davtiani* and *N. archari* was *N. oiratianus* Rajewskaya, 1929 (Table 5). No more than 110 mature male *N. oiratianus* were present in any one of the 36 animals in which it occurred. Among the 50 Kenai sheep, 24 harbored mature male *N. oiratianus*. This nematode occurred in the abomasum of only 1 of 23 sheep (one abomasum was not available), but in the small intestine of 23 of 24 sheep. Only 0.3 percent (1/403) of the male *N. oiratianus* found in the Kenai sheep were in the abomasum, the remaining 99.7 percent (402/403) were in the small intestine (Table 15). In the 12 sheep taken in 1972 and 1973 from Dry Creek, two had *N. oiratianus* males in the abomasum, 3 had them in the duodenum, 10 in the entire small intestine, and 2 in the caecum or colon (Table 16). One percent (2/278) of the total mature male *N. oiratianus* were found in the abomasum,

Table 12. 1972 and 1973 Dry Creek sheep: location of *N. archari*.

Sheep No.	Abo	Duod	As 1	As 2	As 3	As 4	Ant. Sm. A	Jeju	Ant. Sm. Intestine	Post. Sm.	Caecum & Colon
3559	-	7							-	-	-
3578	5	6							16	-	-
3579	1	217							-	6	-
3580	162	34							570	9	-
3581	-	56							4	-	-
3623	-	3							1	-	-
3624	2	14							4	-	-
3695	-	4							3	-	-
3697	3	22							101	2	13
3870	-	1							94	5	-
3893	-	65					350	-		-	300
3894	5	30	680	190	160	100	1130	5	1135	10	-
3895	15	30	100	25	45	10	180	16	196	14	20
3896	-	103							524	133	-
3897	30	5							120	-	-
	223 (5%)	597 (13%)					1660 (77%)	16 (1%)	3118(70%)	179(4%)	333(8%)

Total = 4450 *N. archari*

Table 13. 1964-1971 Kenai Peninsula sheep: location of *N. davtiani*.

Sheep No.	Abomasum	Small Intestine
2735	1	-
2736	-	2
3234	19	4
3235	-	29
3237	1	-
3238	-	9
3242	4	19
3247	1	-
3249	6	1
3252	-	1
3253	-	1
3254	-	2
3255	-	14
3258	-	43
3263	-	1
3264	-	6
3267	-	4
3271	2	13
3272	5	7
3273	-	1
3274	2	2
3331	missing	1
3332	3	3
3333	2	-
Total	46	163

Table 14. 1972 and 1973 Dry Creek sheep: location of *N. davtiani*.

Sheep No.	Abo	Duod	As 1	As 2	As 3	As 4	Ant. Sm. A	Jeju	Ant. Sm. Intestine	Post. Sm.	Caecum & Colon
3578	1	-							1	-	-
3579	-	1							-	-	-
3580	12	5							2	-	-
3581	1	2							2	1	1
3623	-	3							-	-	-
3624	-	1							-	-	-
3697	1	20							2	-	-
3870	-	27							5	-	-
3893	-	1					1	-		-	-
3894	60	145	5	-	-	-		-		4	-
3895	2	4	6	-	-	-		-		-	-
3896	-	99							38	11	-
3897	40	1							5	-	50
	117 (21%)	309 (55%)							67(12%)	16(3%)	51(9%)

Total = 560 *N. davtiani*

Table 15. 1964-1971 Kenai Peninsula sheep: location of *N. oiratianus*.

Sheep No.	Abomasum	Small Intestine
2738	-	3
3234	-	3
3235	-	1
3238	-	1
3242	-	67
3244	-	9
3252	-	1
3253	-	31
3255	-	2
3256	-	39
3258	-	11
3259	-	25
3261	1	-
3263	-	7
3264	-	7
3269	-	5
3271	-	64
3272	-	30
3274	-	13
3275	-	1
3330	missing	35
3331	missing	28
3332	-	18
3338	-	1
Total	1	402

Table 16. 1972 and 1973 Dry Creek sheep: location of *N. oiratianus*.

Sheep No.	Abo	Duod	As 1	As 2	As 3	As 4	Ant. Sm. A	Jeju	Ant. Sm. Intestine	Post. Sm.	Caecum & Colon
3578	-	-							1		-
3579	-	1							-		-
3580	1	-							-	-	-
3581	-	37							19	-	1
3623	-	-							15		-
3624	-	-							1	-	-
3695	-	-							5		-
3697	-	-							96	11	3
3870	1	1							33	1	-
3893	-	-					5	-		-	-
3894	-	-	5	10	5	15	35	-	35	-	-
3895	-	-	-	-	10	-	10	1	11	-	-
	2 (1%)	39 (14%)					50 (91%)	1 (2%)	204 (79%)	12 (5%)	4(1%)

Total = 278 *N. oiratianus*

14 percent (39/278) in the duodenum, 78 percent (200/256) in the anterior half of the small intestine, 5 percent (12/256) in the posterior small intestine, and 1 percent (4/278) in the caecum or colon. When the anterior small intestine of 2 sheep was subdivided, 91 percent of the total *N. oiratianus* males were found in the first 4 meters of the small intestine; 60 percent were found specifically in the third and fourth meters. Therefore, there are some indications that *N. oiratianus* is a parasite of the first four meters of the small intestine, with the majority found in the third and fourth meters.

Nematodirus spathiger (Railliet 1896) Railliet and Henry, 1909 occurred in 30 of the 75 animals examined and numbered up to 431 mature males per sheep (Table 5). Infections of this species tended to be relatively large when they occurred. The average number of *N. spathiger* males was 75 per sheep, a level second only to *N. archari* in this genus. Nineteen of the 50 Kenai Peninsula sheep harbored *N. spathiger*. All 19 were infections of the small intestine only and no *N. spathiger* were found in the abomasum (Table 17). Eleven of 15 sheep taken in 1972 and 1973 at Dry Creek were infected with *N. spathiger* males. Of these, 0.05 percent (1/1837) of the males were in the abomasum, none (0/1827) were found in the duodenum, 42 percent (760/1825) occurred in the anterior half of the small intestine, 53 percent (970/1835) in the posterior small intestine, and 5 percent (94/1837) in the caecum or colon (Table 18). In three sheep the anterior small intestine was halved. Two percent (21/860) of the total mature male *N. spathiger* in these 3 sheep were found in the anterior half ("anterior small intestine A"); 33 percent (286/860) were found in the posterior half ("jejunum"); and 60 percent (518/860) were found in the posterior small intestine. Thus it appears that the posterior 3/4 of the small intestine ("jejunum" plus posterior half of small intestine) usually contains about 93 percent of the mature *N. spathiger*.

(e) *Nematodirella* Yorke and Maplestone, 1926

Only 2 of the 74 sheep examined harbored *Nematodirella* spp. Preliminary examination of the specimens indicates they are probably *N. longispiculata* Yorke and Maplestone, 1926, the species previously reported for Alaskan moose (*Alces alces*) (Neiland 1961, 1962 and 1963). However, because of the confusion and overlap of species in this genus, a definite identification of the specimens will be made after the numerous trichostrongylid specimens on hand from moose, bison (*Bison bison*) and other ungulates are examined. Both sheep harboring male *Nematodirella* were collected at Dry Creek in early April 1973. A 2-year-old ewe had 7 specimens in her caecum and colon, while a 7-year-old ewe had 20 in the posterior half of the small intestine, 55 in the caecum and 60 in the colon. Because 86 percent (122/142) of the *Nematodirella* were found in the caecum or colon, this appears to be their preferred location. However, it is also possible that the nematodes were accidentally acquired from moose and were being passed out of the gastrointestinal tract when found in its lower part, a supposition which is supported by the fact that in moose and domestic sheep *Nematodirella* occurs primarily in the small intestine.

Table 17. 1964-1971 Kenai Peninsula sheep: location of *N. spathiger*.

Sheep No.	Abomasum	Small Intestine
3234	-	1
3242	-	42
3243	-	1
3244	-	10
3249	-	3
3253	-	4
3255	-	17
3256	-	2
3258	-	4
3261	-	1
3262	-	4
3263	-	14
3269	-	1
3271	-	97
3272	-	1
3274	-	8
3277	-	1
3331	missing	23
3332	-	2
Total	0	236

Table 18. 1972 and 1973 Dry Creek sheep: location of *N. spathiger*.

Sheep No.	Abo	Duod	As 1	As 2	As 3	As 4	Ant. Sm. A	Jeju	Ant. Sm. Intestine	Post. Sm.	Caecum & Colon
3575	–	–							10	–	–
3580	–	–							60	9	–
3695	–	–								2	–
3696	–	–							4	–	–
3697	–	–							1	16	–
3870	–	–							179	23	–
3893	–	–					20	20	40	35	10
3894	–	–					–	120	120	290	–
3895	–	–	–	–	1	–		146	147	245	25
3896	1	–							54	184	3
3897	–	–							155	220	56
	1 (.05%)	0 (–)					21 (2%)	286(33%)	760 (42%)	970(53%)	94(5%)

Total = 1837 *N. spathiger*

3. Trichostrongylid Burden by Month

For a variety of reasons, collections of the 75 sheep examined were unevenly distributed through the year; 77 percent (58/75) were collected between November and April and 23 percent (17/75) were collected between May and October (Table 19). There is little comparative information for the late summer and autumn period not only because of the relatively few sheep collected, but also because for 7 of the 17 sheep in this period the specimens were collected under field conditions. No sheep at all were collected in the months of October and December, and only one animal was collected in September.

Besides being unevenly distributed over the months, the sheep collections were also made in different years and important differences in weather, snow depth, and other conditions might exist between the same or adjacent months which were sampled in different years. There were also seasonal differences for the collection of sheep groups: all 50 sheep taken during 1970-1971 on the Kenai Peninsula were collected in November and January through April, while almost all the 18 sheep taken during 1972 and 1973 in Dry Creek were collected from April through July. Almost all the eight sheep taken in miscellaneous locations were collected from July through September. Therefore, it is difficult to get a proper overview of the dynamics of the trichostrongylid population both as a whole and by genus and species, since each third of the year is essentially represented by a group from a different locality.

Examining these data by locality, the collection on the Kenai Peninsula in 1970-1971 covers the winter and early spring period (Table 20). There seem to be fewer trichostrongylids among the nine sheep collected in November than among those taken January through April.

In particular, no representatives of the genus *Ostertagia* were seen in the collection made in November but small numbers were present in the collections made in January, February, March and April. It also appears that all species of *Nematodirus* were more abundant in March and April than in November or January.

The collections in 1972 and 1973 in Dry Creek cover the period from March through July, and include an additional two sheep taken in November (Table 21). The average number of mature trichostrongylids was 880 (n=2) in November, 749 (n=1) in March, 3450 (n=5) in April, 1903 (n=4) in May, 514 (n=2) in June and 1356 (n=3) in July. In contrast to the Kenai collection, there did not appear to be fewer trichostrongylids in November than in March or even June. Large numbers of *Marshallagia marshalli, Nematodirus archari* and *N. spathiger* account for the big average load for April, and for the moderate May load. In June and July, however, species of *Ostertagia*, particularly *O. circumcincta*, account for nearly half the burden, while species of *Nematodirus* are relatively less abundant. A few *Ostertagia* were present in the sheep taken in November, although they were absent in the Kenai sheep. Also in contrast to the Kenai collection, the sheep collected in Dry Creek in November had *Nematodirus* numbers comparable with sheep taken in June and July.

Table 19. Total species burdens by month on all sheep examined.

No. Sheep	7	9	13	18	6	2	5	3	1	-	11	-	Total 75
Month	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	Nov	Dec	
Mature males													
M. marshalli	226	557	1920	4136	2204	229	721	84	74	-	573	-	10,724
O. circumcincta	-	-	-	2	6	158	704	-	-	-	-	-	870
O. occidentalis	3	2	21	43	72	16	96	7	1	-	9	-	268
O. ostertagi	-	-	-	-	-	-	22	2	-	-	-	-	24
O. trifurcata	-	-	-	-	7	37	100	1	-	-	-	-	145
All *Ostertagia* spp.	3	2	21	45	85	211	922	10	1	-	9	-	1307
T. davtiani	-	-	-	-	3	24	36	-	-	-	-	-	63
N. archari	27	28	177	3207	1086	24	148	-	-	-	117	-	4814
N. davtiani	5	59	97	516	29	4	23	-	-	-	36	-	769
N. oiratianus	32	6	171	203	60	16	115	1	-	-	77	-	681
N. spathiger	22	5	127	1600	69	-	23	-	-	-	217	-	2063
Nematodirus spp. unidentified	1	-	-	-	3	-	2	-	-	-	-	-	6
All *Nematodirus* spp.	87	98	572	5526	1247	44	311	1	-	-	447	-	8333
Nematodirella spp.	-	-	-	128	-	-	-	-	-	-	-	-	128
Total males	316	657	2513	9835	3539	508	1990	95	75	-	1029	-	20,557
Total all females	75	621	3780	9182	4089	519	2085	288	231	-	1045	-	21,911
Total mature trichostrongylids	391	1278	6293	19,017	7628	1027	4075	383	306	-	2074	-	42,468

Table 20. 1970-1971 Kenai Peninsula sheep: total and species burdens by month.

No. Sheep	7	9	12	13	-	-	-	-	-	-	9	-	Total 50
Month	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	Nov	Dec	
Mature males													
M. marshalli	226	557	1747	386	-	-	-	-	-	-	88	-	3004
O. circumcincta	-	-	-	2	-	-	-	-	-	-	-	-	2
O. occidentalis	3	2	17	1	-	-	-	-	-	-	-	-	23
O. ostertagi	-	-	-	-	-	-	-	-	-	-	-	-	-
O. trifurcata	-	-	-	-	-	-	-	-	-	-	-	-	-
All *Ostertagia* spp.	3	2	17	3	-	-	-	-	-	-	-	-	25
T. davtiani	-	-	-	-	-	-	-	-	-	-	-	-	-
N. archari	27	28	170	122	-	-	-	-	-	-	17	-	364
N. davtiani	5	59	97	44	-	-	-	-	-	-	4	-	209
N. oiratianus	32	6	171	152	-	-	-	-	-	-	41	-	402
N. spathiger	22	5	127	67	-	-	-	-	-	-	15	-	236
Nematodirus spp. unidentified	1	-	-	-	-	-	-	-	-	-	-	-	1
All *Nematodirus* spp.	87	98	565	385	-	-	-	-	-	-	77	-	1212
Nematodirella spp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Total males	316	657	2329	774	-	-	-	-	-	-	165	-	4241
Total all females	75	621	3215	992	-	-	-	-	-	-	150	-	5053
Total mature trichostrongylids	391	1278	5544	1766	-	-	-	-	-	-	315	-	9294

Table 21. 1972-1973 Dry Creek sheep: total and species burdens by month.

No. Sheep (#3575 omitted)	–	–	1	5	4	2	3	–	–	–	2	–	Total 15
Month	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	Nov	Dec	
Mature males													
M. marshalli	–	–	173	3750	2202	229	719	–	–	–	485	–	7558
O. circumcincta	–	–	–	–	6	158	703	–	–	–	–	–	867
O. occidentalis	–	–	4	42	72	16	96	–	–	–	9	–	239
O. ostertagi	–	–	–	–	–	–	22	–	–	–	–	–	22
O. trifurcata	–	–	–	–	7	37	100	–	–	–	–	–	144
All *Ostertagia* spp.	–	–	4	42	85	211	921	–	–	–	9	–	1272
T. davtiani	–	–	–	–	3	24	36	–	–	–	–	–	63
N. archari	–	–	7	3085	1086	24	148	–	–	–	100	–	4450
N. davtiani	–	–	–	472	29	4	23	–	–	–	32	–	560
N. oiratianus	–	–	–	51	60	16	115	–	–	–	36	–	278
N. spathiger	–	–	–	1533	69	–	23	–	–	–	202	–	1827
Nematodirus spp. unidentified	–	–	–	–	3	–	2	–	–	–	–	–	5
All *Nematodirus* spp.	–	–	7	5141	1247	44	311	–	–	–	370	–	7120
Nematodirella spp.	–	–	–	128	–	–	–	–	–	–	–	–	128
Total males	–	–	184	9061	3537	508	1987	–	–	–	864	–	16,141
Total all females	–	–	565	8190	4075	519	2080	–	–	–	895	–	16,320
Total mature trichostrongylids	–	–	749	17,251	7612	1027	4067	–	–	–	1759	–	32,461

The eight Dall sheep collected at miscellaneous locations during 1964-1973 (Table 22) are generally difficult to compare by month because few specimens were recovered. Therefore these sheep are not very indicative of trichostrongylid population dynamics. *Marshallagia marshalli* was present in all sheep but a six-week-old lamb. A few *Ostertagia* were seen in July, August and September, and a single *Nematodirus* was seen in August.

Despite differences in sampling time, locality and procedure, a few general trends for the population dynamics of trichostrongylids over the course of 12 months can still be noted: 1) trichostrongylids are present in the sheep population in at least modest numbers during the entire year; 2) *Marshallagia marshalli* and *Ostertagia occidentalis* are common year-round, with the former present in abundant numbers while the latter is represented by only a few specimens; and 3) species of *Nematodirus* are also common and often abundant in the winter, spring and early summer, but their occurrence in late summer and autumn has not yet been substantiated.

4. Variations of Trichostrongylid Burdens by Age of Host and Season

Of the 75 sheep examined fully, 12 were collected between 6 weeks and 1 year of age, 16 between 1 and 2 years, 15 between 2 and 4 years, 16 between 5 and 7 years and 16 between 8 and 14 years. The total species-burden for each age class is given in Table 23. The 5-7 years age class contained the largest number of mature trichostrongylids: contributing to this are the large numbers of *Marshallagia marshalli* and *Nematodirus archari* seen in the 5 Dry Creek sheep in this age class. The 2-4 years age class includes a large number of *Ostertagia* species. However, this is primarily the effect of a single, large *O. circumcincta* infection in a 4-year-old ewe taken in 1972 in Dry Creek. The number of specimens of *Ostertagia* encountered in the 0-1 year age class is surprisingly small, but all but one of these young animals were collected during the winter and early spring. Species of *Ostertagia* were not generally seen in moderate numbers until the late spring collections. The same reasoning could also explain the low numbers of *Nematodirus* in the 0-1 year age class. However, the 2-4 year age class also had a small number of *Nematodirus*, primarily due to the low numbers of *N. archari* encountered in the sheep taken in 1972 in Dry Creek. In general, there were no clear indications from these grouped data that certain age classes harbor more trichostrongylids than other age classes.

Table 24 presents the cumulative trichostrongylid burden by age class for each of the three collections, i.e. those from the Kenai Peninsula, Dry Creek and miscellaneous localities (It can be immediately seen that the intensive recovery techniques used on the 1972 and 1973 sheep resulted in many more specimens, and the variations in these 17 sheep exert disproportionate influence when combined with sheep from other localities as in Table 23). For sheep from the Kenai Peninsula, the 0-1 year age class had the largest burden of mature trichostrongylids ($\bar{x}$ = 397, n=11) while the older classes have burdens similar to each other ($\bar{x}$ = 129, 173, 113 and 88 [Table 25]). No sheep in the 0-1 year age class were collected at Dry Creek. The lowest average burden was

Table 22. 1964-1973 sheep from miscellaneous locations: total and species burdens by month.

No. Sheep	–	–	–	–	2	–	2	3	1	–	–	–	Total 8
Month	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	Nov	Dec	
Mature males													
M. marshalli	–	–	–	–	2	–	2	84	74	–	–	–	162
O. circumcincta	–	–	–	–	–	–	–	–	–	–	–	–	–
O. occidentalis	–	–	–	–	–	–	1	7	1	–	–	–	9
O. ostertagi	–	–	–	–	–	–	–	2	–	–	–	–	2
O. trifurcata	–	–	–	–	–	–	–	1	–	–	–	–	1
All *Ostertagia* spp.	–	–	–	–	–	–	1	10	1	–	–	–	12
T. davtiani	–	–	–	–	–	–	–	–	–	–	–	–	–
N. archari	–	–	–	–	–	–	–	–	–	–	–	–	–
N. davtiani	–	–	–	–	–	–	–	–	–	–	–	–	–
N. oiratianus	–	–	–	–	–	–	–	1	–	–	–	–	1
N. spathiger	–	–	–	–	–	–	–	–	–	–	–	–	–
All *Nematodirus* spp.	–	–	–	–	–	–	–	1	–	–	–	–	1
Nematodirella spp.	–	–	–	–	–	–	–	–	–	–	–	–	–
Total males	–	–	–	–	2	–	3	95	75	–	–	–	175
Total all females	–	–	–	–	14	–	5	288	231	–	–	–	538
Total mature trichostrongylids	–	–	–	–	16	–	8	383	306	–	–	–	713

Table 23. Trichostrongylids burden by age class (all locations).

	0-1 yr. n=12	1-2 yr. n=16	2-4 yr. n=15	5-7 yr. n=16	8-14 yr. n=16	Total n=75
Mature males						
M. marshalli	1156	1777	1795	2893	3103	10,724
O. circumcincta	1	128	604	3	132	868
O. occidentalis	18	82	74	61	37	272
O. ostertagi	-	22	-	-	2	24
O. trifurcata	-	28	82	5	30	145
All *Ostertagia* spp.	19	260	760	69	201	1309
T. davtiani	-	15	28	3	17	63
N. archari	176	1285	204	1582	1567	4814
N. davtiani	61	249	63	214	182	769
N. oiratianus	235	191	148	97	10	681
N. spathiger	211	422	25	1072	333	2063
Nematodirus spp. unidentified	-	-	3	2	1	6
All *Nematodirus* spp.	683	2147	443	2967	2093	8333
Nematodirella spp.	-	7	-	121	-	128
Total males	1858	4206	3026	6053	5414	20,557
Total all females	2506	3977	3316	6184	5928	21,911
Total mature trichostrongylids	4364	8183	6342	12,237	11,342	42,468

Table 24. Trichostrongylids burden by age class and locality.

	0 - 1 yr.			1 - 2 yr.			2 - 4 yr.		
	1970-71 Kenai n=11	1972-73 Dry Cr. n=0	1964-73 Misc. n=1	1970-71 Kenai n=12	1972-73 Dry Cr. n=4	1964-73 Misc. n=0	1970-71 Kenai n=9	1972-73 Dry Cr. n=4	1964-73 Misc. n=2
Mature males									
M. marshalli	1156	-	-	569	1208	-	680	1039	76
O. circumcincta	1	-	-	-	128	-	-	604	-
O. occidentalis	18	-	-	-	82	-	5	67	2
O. ostertagi	-	-	-	-	22	-	-	-	-
O. trifurcata	-	-	-	-	28	-	-	82	-
All *Ostertagia* spp.	19	-	-	-	260	-	5	753	2
T. davtiani	-	-	-	-	15	-	-	28	-
N. archari	176	-	-	34	1251	-	29	175	-
N. davtiani	61	-	-	25	224	-	38	25	-
N. oiratianus	235	-	-	79	112	-	37	111	-
N. spathiger	211	-	-	10	412	-	8	17	-
Nematodirus spp. unidentified		-	-	-	-	-	-	3	-
All *Nematodirus* spp.	683	-	-	148	1999	-	112	331	-
Nematodirella spp.	-	-	-	-	7	-	-	-	-
Total males	1858	-	-	717	3489	-	797	2151	78
Total all females	2505	-	1	826	3151	-	761	2320	235
Total mature trichostrongylids	4363	-	1	1543	6640	-	1558	4471	313

Table 24. Continued.

	5 - 7 yr.			8 - 4 yr.			Total		
	1970-71 Kenai n=10	1972-73 Dry Cr. n=5	1964-73 Misc. n=1	1970-71 Kenai n=8	1972-73 Dry Cr. n=4	1964-73 Misc. n=4	1970-71 Kenai n=50	1972-73 Dry Cr. n=17	1964-73 Misc. n=8
Mature males									
M. marshalli	320	2534	39	279	2777	47	3004	7558	162
O. circumcincta	-	3	-	-	132	-	1	867	-
O. occidentalis	1	60	-	-	30	7	24	239	9
O. ostertagi	-	-	-	-	-	2	-	22	2
O. trifurcata	-	4	1	-	30	-	-	144	1
All *Ostertagia* spp.	1	67	1	-	192	9	25	1272	12
T. davtiani	-	3	-	-	17	-	-	63	-
N. archari	53	1529	-	72	1495	-	364	4450	-
N. davtiani	54	160	-	31	151	-	209	560	-
N. oiratianus	48	49	-	3	6	1	402	278	1
N. spathiger	5	1067	-	2	331	-	236	1827	-
N. spp. unidentified	-	2	-	1	-	-	1	5	-
All *Nematodirus* spp.	160	2807	-	109	1983	1	1212	7125	1
Nematodirella spp.	-	121	-	-	-	-	-	128	-
Total males	481	5532	40	388	4969	57	4241	16,141	175
Total all females	647	5489	48	314	5360	254	5053	16,320	538
Total mature trichostrongylids	1128	11,021	88	702	10,329	311	9294	32,461	713

Table 25. 1970-1971 Kenai Peninsula sheep by sheep age and month of collection.

Sheep No.	3244	3250	3252	3255	3262	3256	3263	3271	3331	3332	3242	
Sex & Age	1/2 M	1/2 M	1/2 M	1/2 M	1/2 F	3/4 F	3/4 M	3/4 M	1 F	1 M	1 F	0-1 yr.
Date	11/13/70	11/13/70	11/13/70	1/14/71	1/14/71	3/18/71	3/18/71	3/18/71	4/27/71	4/27/71	4/27/71	n=11
Mature males												
M. marshalli	-	5	2	55	14	108	320	579	-*	42	31	1156
O. circumcincta	-	-	-	-	-	-	-	-	-*	1	-	1
O. occidentalis	-	-	-	2	-	1	2	12	-*	-	1	18
O. ostertagi	-	-	-	-	-	-	-	-	-*	-	-	-
O. trifurcata	-	-	-	-	-	-	-	-	-*	-	-	-
All *Ostertagia* spp.	-	-	-	2	-	1	2	12	-*	1	1	19
T. davtiani	-	-	-	-	-	-	-	-	-*	-	-	-
N. archari	1	-	-	-	-	15	3	74	39	7	37	176
N. davtiani	-	-	1	-	-	14	1	15	1	6	23	61
N. oiratianus	9	-	1	2	-	39	7	64	28	18	67	235
N. spathiger	10	-	-	17	4	2	14	97	23	2	42	211
All *Nematodirus* spp.	20	-	2	19	4	70	25	250	91	33	169	683
Nematodirella spp.	-	-	-	-	-	-	-	-	-	-	-	-
Total males	20	5	4	76	18	179	347	841	91*	76	201	1858
Total all females	39	25	12	14	5	317	557	1069	71	125	271	2505
Total mature trichostrongylids	59	30	16	90	23	496	904	1910	162	201	472	4363

* abomasum missing

Table 25. Continued.

Sheep No. Sex & Age Date	3259 1 1/2 M 1/14/71	3273 1 1/2 M 1/14/71	3236 1 1/2 M 2/26/71	3275 1 3/4 F 2/26/71	3264 1 3/4 M 3/18/71	3272 1 3/4 F 3/18/71	3274 1 3/4 F 3/18/71	3277 1 3/4 M 3/18/71	2736 2 F 4/28/70	2738 2 F 4/28/70	3240 2 M 4/27/71	3248 2 M 4/27/71	1-2 yr. n=12
Mature males													
M. marshalli	11	38	8	1	53	23	15	252	14	2	43	109	569
O. circumcincta	-	-	-	-	-	-	-	-	-	-	-	-	-
O. occidentalis	-	-	-	-	-	-	-	-	-	-	-	-	-
O. ostertagi	-	-	-	-	-	-	-	-	-	-	-	-	-
O. trifurcata	-	-	-	-	-	-	-	-	-	-	-	-	-
All *Ostertagia* spp.	-	-	-	-	-	-	-	-	-	-	-	-	-
T. davtiani	-	-	-	-	-	-	-	-	-	-	-	-	-
N. archari	2	-	-	-	12	5	4	-	-	-	9	2	34
N. davtiani	-	1	-	-	6	12	4	-	2	-	-	-	25
N. oiratianus	25	-	-	1	7	30	13	-	-	3	-	-	79
N. spathiger	-	-	-	-	-	1	8	1	-	-	-	-	10
All *Nematodirus* spp.	27	1	-	1	25	48	29	1	2	3	9	2	148
Nematodirella spp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Total males	38	39	8	2	78	71	44	253	16	5	52	111	717
Total all females	4	7	-	-	16	7	151	323	139	7	-	172	826
Total mature trichostrongylids	42	46	8	2	94	78	195	576	155	12	52	283	1543

Table 25. Continued.

Sheep No. Sex & Age Date	3247 2 1/2 F 11/13/70	3253 2 1/2 F 11/13/70	3251 3 1/2 F 11/13/70	3269 3 1/2 F 1/14/71	3235 2 1/2 F 2/26/71	3239 2 3/4 F 2/26/71	3268 2 3/4 M 2/26/71	3249 3 3/4 M 2/26/71	3266 3 3/4 F 3/18/71	2-4 yrs. n=9
Mature males										
M. marshalli	7	54	7	32	7	306	23	67	177	680
O. circumcincta	-	-	-	-	-	-	-	-	-	-
O. occidentalis	-	-	-	1	-	2	-	-	2	5
O. ostertagi	-	-	-	-	-	-	-	-	-	-
O. trifurcata	-	-	-	-	-	-	-	-	-	-
All *Ostertagia* spp.	-	-	-	1	-	2	-	-	2	5
T. davtiani	-	-	-	-	-	-	-	-	-	-
N. archari	1	15	-	-	11	-	-	2	-	29
N. davtiani	1	1	-	-	29	-	-	7	-	38
N. oiratianus	-	31	-	5	1	-	-	-	-	37
N. spathiger	-	4	-	1	-	-	-	3	-	8
All *Nematodirus* spp.	2	51	-	6	41	-	-	12	-	112
Nematodirella spp.	-	-	-	-	-	-	-	-	-	-
Total males	9	105	7	39	48	308	23	79	179	797
Total all females	12	15	27	12	15	310	32	75	263	761
Total mature trichostrongylids	21	120	34	51	63	618	55	154	442	1558

Table 25. Continued.

Sheep No. Sex & Age Date	3237 6 1/2 F 11/13/70	3241 7 1/2 F 11/13/70	3270 6 1/2 F 1/14/71	3261 6 3/4 F 2/26/71	3258 5 3/4 F 3/18/71	3257 7+ F 3/18/71	3330 5 F 4/27/71	3245 5 F 4/27/71	3238 6 F 4/27/71	2735 7 F 4/28/70	5-7 yrs. n=10
Mature males											
M. marshalli	3	2	25	2	77	81	-	54	47	29	320
O. circumcincta	-	-	-	-	-	-	-	-	-	-	-
O. occidentalis	-	-	-	-	-	-	-	-	-	1	1
O. ostertagi	-	-	-	-	-	-	-	-	-	-	-
O. trifurcata	-	-	-	-	-	-	-	-	-	-	-
All *Ostertagia* spp.	-	-	-	-	-	-	-	-	-	1	1
T. davtiani	-	-	-	-	-	-	-	-	-	-	-
N. archari	-	-	3	1	20	2	7	3	14	3	53
N. davtiani	1	-	-	-	43	-	-	-	9	1	54
N. oiratianus	-	-	-	1	11	-	35	-	1	-	48
N. spathiger	-	-	-	1	4	-	-	-	-	-	5
All *Nematodirus* spp.	1	-	3	3	78	2	42	3	24	4	160
Nematodirella spp.	-	-	-	-	-	-	-	-	-	-	-
Total males	4	2	28	5	155	83	42	57	71	34	481
Total all females	1	-	17	6	291	193	4	59	7	69	647
Total mature trichostrongylids	5	2	45	11	446	276	46	116	78	103	1128

Table 25. Continued.

Sheep No. Sex & Age Date	3243 8 1/2 F 11/13/70	3267 8 1/2 F 1/14/71	3234 9 1/2 F 2/26/71	3276 13 1/2 F 2/26/71	3265 9 3/4 F 3/18/71	3254 10 3/4 F 3/18/71	2737 10 F 4/28/70	3333 11 F 4/27/71	8-14 yrs. n=8
Mature males									
M. marshalli	8	51	97	46	6	56	9	6	279
O. circumcincta	-	-	-	-	-	-	-	-	-
O. occidentalis	-	-	-	-	-	-	-	-	-
O. ostertagi	-	-	-	-	-	-	-	-	-
O. trifurcata	-	-	-	-	-	-	-	-	-
All *Ostertagia spp.*	-	-	-	-	-	-	-	-	-
T. davtiani	-	-	-	-	-	-	-	-	-
N. archari	-	22	14	-	-	35	-	1	72
N. davtiani	-	4	23	-	-	2	-	2	31
N. oiratianus	-	-	3	-	-	-	-	-	3
N. spathiger	1	-	1	-	-	-	-	-	2
Nematodirus spp. unidentified		1							1
All *Nematodirus* spp.	1	27	41	-	-	37	-	3	109
Nematodirella spp.	-	-	-	-	-	-	-	-	-
Total males	9	78	138	46	6	93	9	9	388
Total all females	19	16	173	10	17	11	60	8	314
Total mature trichostrongylids	28	94	311	56	23	104	69	17	702

encountered among the 2-4-year olds ($\bar{x}$ = 1118, n=4) while the 1-2-year olds were somewhat higher ($\bar{x}$ = 1660, n=4) and the older age classes had large and similar numbers of mature helminths ($\bar{x}$ = 2204, 2582 [Table 26]). The burdens seen in the various age classes of sheep from miscellaneous locations were similar, but the information is too sparse to justify consideration by classes (Table 27).

The trichostrongylid burden vs. age class information on the sheep from the Kenai and Dry Creek study areas appears to be contradictory, but it should be recalled that all the collections on the Kenai were made during winter and early spring, while the collections at Dry Creek were made in late spring and early summer. A careful examination of the records of individual animals collected on the Kenai Peninsula (Table 25) reveals that in March the numbers of mature trichostrongylids increased to moderate numbers in all (6/6) of the lambs, but in only 37 percent (7/19) of the yearlings and older animals. Of the 6 animals taken at Dry Creek which harbored more than 2,000 mature trichostrongylids, 4 were sheep older than 5 years which were taken in April and May (Table 26).

Among sheep older than a year, there appears to be considerable variation in whether or not a substantial increase in the mature trichostrongylid burden occurs sometime during March, April or May. This phenomenon, well known in domestic sheep as the "spring rise", will be discussed later in this report. Material from lambs (i.e. sheep younger than one year) taken on the Kenai indicates that all members of this age class experience a large increase in trichostrongylid burden in early spring (March). Probably the greatest significance of data from animals from the Kenai is that lambs, which have low resistance to trichostrongylids, inevitably are subjected to a "spring rise," whereas older animals in good condition can reduce or repel the increase in numbers of worms.

5. Trichostrongylid Burden vs. Host Condition

(a) Body weight and marrow fat of the host

Nichols (Nichols and Heimer 1972) has reported the body weights of all 50 sheep taken in 1970-1971 on the Kenai Peninsula and Heimer (1973) has reported the weights of 17 of the 18 sheep (only part of one sheep, #3575, was available for necropsy) taken in 1972-1973 at Dry Creek. The numbers of trichostrongylids are listed together with the body weight for each animal in Tables 28 (Kenai) and 29 (Dry Creek), with the sheep arranged in order of increasing weight. Although there is a wide sample of different sheep weights, a careful examination reveals no clear relationship between body weight and total trichostrongylid burden in either the animals from Kenai or Dry Creek. However, when the body weights of sheep from Dry Creek were examined in relation to particular species of parasites, there was some indication that species of *Ostertagia* were more prevalent and abundant in lighter-weight sheep (less than 105 pounds). Of course the comparison is biased because lighter-weight sheep are young animals. Thus, these results suggest that *Ostertagia* infections appear in young animals which perhaps lack acquired resistance to infection. In contrast, *Nematodirus spathiger* was more prevalent and was found in higher numbers in sheep weighing more than 105 pounds.

Table 26. 1972-1973 Dry Creek sheep by sheep age and month of collection.

Sheep No. / Sex & Age / Date	(0-1yr) none	3581 1 F 5/4/72	3623 1 F 6/5/72	3695 1 M 7/9/72	3894 2 F 4/10/73	(1-2yr) n=4	3868 3 F 11/17/72	3559 4 F 3/18/72	3578 4 F 5/5/72	3697 4 F 7/9/72	(2-4yr) n=4
Mature males											
M. marshalli	-	281	51	485	391	1208	184	173	455	227	1039
O. circumcincta	-	1	46	81	-	128	-	-	2	602	604
O. occidentalis	-	15	10	42	15	82	1	4	10	52	67
O. ostertagi	-	-	-	22	-	22	-	-	-	-	-
O. trifurcata	-	-	11	17	-	28	-	-	3	79	82
All *Ostertagia* spp.	-	16	67	162	15	260	1	4	15	733	753
T. davtiani	-	-	9	6	-	15	-	-	-	28	28
N. archari	-	60	4	7	1180	1251	-	7	27	141	175
N. davtiani	-	7	3	-	214	224	-	-	2	23	25
N. oiratianus	-	57	15	5	35	112	-	-	1	110	111
N. spathiger	-	-	-	2	410	412	-	-	-	17	17
Nematodirus spp. unidentified	-	-	-	-	-	-	-	-	1	2	3
All *Nematodirus* spp.	-	124	22	14	1839	1999	-	7	31	293	331
Nematodirella spp.	-	-	-	-	7	7	-	-	-	-	-
Total males	-	421	149	667	2252	3489	185	184	501	1281	2151
Total all females	-	430	160	905	1656	3151	190	565	480	1085	2320
Total mature trichostrongylids	-	851	309	1572	3908	6640	375	749	981	2366	4471

Table 26. Continued.

Sheep No. Age & Sex Date	3870 5 F 11/17/72	3897 5 F 4/10/73	3895 7 F 4/10/73	3579 7 F 5/5/72	3580 7 F 5/5/72	(5-7yr) n=5	3893 8 F 4/10/73	3896 8 F 4/10/73	3696 11 F 7/9/72	3624 13 F 6/5/72	(8-14yr) n=4	Total all Ages
Mature males												
M. marshalli	301	210	557	704	762	2534	565	2027	7	178	2777	7558
O. circumcincta	-	-	-	-	3	3	-	-	20	112	132	867
O. occidentalis	8	-	5	28	19	60	-	22	2	6	30	239
O. ostertagi	-	-	-	-	-	-	-	-	-	-	-	22
O. trifurcata	-	-	-	-	4	4	-	-	4	26	30	144
All *Ostertagia* spp.	8	-	5	28	26	67	-	22	26	144	192	1272
T. davtiani	-	-	-	1	2	3	-	-	2	15	17	63
N. archari	100	155	275	224	775	1529	715	760	-	20	1495	4450
N. davtiani	32	96	12	1	19	160	2	148	-	1	151	560
N. oiratianus	36	-	11	1	1	49	5	-	-	1	6	278
N. spathiger	202	431	365	-	69	1067	85	242	4	-	331	1827
Nematodirus spp. unidentified		-	-	-	2	2	-	-	-	-	-	5
All *Nematodirus* spp.	370	682	663	226	866	2807	807	1150	4	22	1983	7125
Nematodirella spp.	-	-	121	-	-	121	-	-	-	-	-	128
Total males	679	892	1346	959	1656	5532	1372	3199	39	359	4969	16,141
Total all females	705	510	1109	895	2270	5489	1390	3525	90	355	5360	16,320
Total mature trichostrongylids	1384	1402	2455	1854	3926	11,021	2762	6724	129	714	10,329	32,461

Table 27. 1964-1973 sheep from miscellaneous locations by sheep age and month of collection.

Sheep No. / Age & Sex / Date	3910 6 wks female 7/18/73	(0-1yr) n=1	(1-2yr) n=0	2576 3 F 7/26/69	7002 3 M 9/23/64	(2-4yr) n=2	3334 6 F 8/4/71	(5-7yr) n=1	3170 9 M 5/15/71	2037 9+ F 5/18/65	3338 9+ M 8/11/71	3339 10 M 8/11/71	(8-14yrs) n=4	Total
Mature males														
M. marshalli	-	-	-	2	74	76	39	-	1	1	3	42	47	162
O. circumcincta	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. occidentalis	-	-	-	1	1	2	-	-	-	-	-	7	7	9
O. ostertagi	-	-	-	-	-	-	-	-	-	-	-	2	2	2
O. trifurcata	-	-	-	-	-	-	1	-	-	-	-	-	-	1
All *Ostertagia* spp.	-	-	-	1	1	2	1	-	-	-	-	9	9	12
T. davtiani	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. archari	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. davtiani	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. oiratianus	-	-	-	-	-	-	-	-	-	-	1	-	1	1
N. spathiger	-	-	-	-	-	-	-	-	-	-	-	-	-	-
All *Nematodirus* spp.	-	-	-	-	-	-	-	-	-	-	1	-	1	1
Nematodirella spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total males	-	-	-	3	75	78	40	-	1	1	4	51	57	175
Total all females	1	-	-	4	231	235	48	-	6	8	9	231	254	538
Total mature trichostrongylids	1	-	-	7	306	313	88	-	7	9	13	282	311	713

Table 28. 1970-1971 Kenai Peninsula sheep: body weight vs. total mature trichostrongylid burden.

Number	Weight	Trichostrongylids
3242	34	472
3331	34	162
3271	41	1910
3263	44	904
2738	45	12
2736	48	155
3332	50	201
3256	55	496
3248	59	283
3250	60	30
3262	61	23
3244	65	59
3255	66	90
3277	69	576
3264	71	94
3274	71	65
3252	74	16
3240	75	52
3235	83	63
2737	85	69
3275	87	2
2735	88	103
3272	89	78
3253	91	120
3273	94	46
3236	99	8
3257	99	276
3330	99	46
3245	101	116
3267	102	94
3259	103	42
3266	103	442
3268	103	55
3254	108	104
3239	110	618
3261	110	11
3269	111	51
3238	114	78
3234	118	311
3265	119	23
3237	120	5
3258	121	446
3247	122	21
3270	123	45
3276	123	56
3333	127	17
3251	129	34
3243	139	28
3241	144	2
3249	152	154

Table 29. 1972-1973 Dry Creek sheep: body weight vs. total mature trichostrongylid burden.

Accession No.*	Weight	Total Mature Trichostrongylids
3695	55	1572
3581	64	851
3623	67	309
3578	80	981
3697	80	2366
3559	88	749
3579	92	3928
3894	95	3908
3624	105	714
3897	105	1402
3696	107	129
3868	107	375
3893	107	2762
3580	109	3926
3896	110	6724
3895	116	2455
3870	132	1384

* #3575 omitted because only part of sheep available for necropsy.

Both Nichols (Nichols and Heimer 1972) and Heimer (1973) have also given marrow fat percentage data for the sheep from the Kenai and Dry Creek areas. Marrow fat percentages obtained, as described by Neiland (1970), serve to indicate the general caloric balance of the animal. A low percentage of marrow fat indicates mobilization of the body energy reserves under prolonged conditions of negative energy balance (Riney 1955). Nichols (Nichols and Heimer 1972) hypothesized that marrow fat levels below 10 percent probably indicate imminent death by starvation. Tables 30 and 31 compare marrow fat percentages with total trichostrongylid burdens of animals from the Kenai and Dry Creek, with these data arranged in order of increasing marrow fat percentage. Again, although there was a wide sample of different marrow fat percentages, unequivocal direct or inverse relationships were not seen between marrow fat percentages and total mature trichostrongylid burdens in animals either from the Kenai or Dry Creek. However, when sheep from Dry Creek were carefully examined in relation to particular nematode species, it was apparent that animals with low marrow-fat percentages (less than 70%) tended to have more intense infections of *Ostertagia*, while animals with more than 96 percent marrow fat tended to have more *Nematodirus spathiger*.

These findings are consistent with those for body weight, indicating that smaller (primarily younger) sheep with low marrow fat harbor *Ostertagia* while heavier sheep with substantial marrow fat harbor *Nematodirus spathiger*. It might be expected that since the parameters of body weight and marrow fat do not vary independently, as discussed below, the same animals with many *Ostertagia* or *N. spathiger* are appearing in both sets of data. However, there is overlap in only slightly more than half the cases. Eight of the 13 animals with moderate numbers of *Ostertagia* have both low body weights and low percentages of marrow fat, while the remaining five meet only one of these conditions. Four of eight sheep with moderate *N. spathiger* numbers have both high weights and high percentages of marrow fat, while the remaining four show only one or the other condition. This implies that all sheep with minimal resistence, whether due to youth or to poor condition, tend to be infected by *Ostertagia*. In a similar way, sheep in good condition or with resistance to infections, including *Ostertagia*, appear to harbor *N. spathiger*. The explanation of this phenomenon is probably found in the immunogenic, pathogenic and epidemiological characteristics of the species involved. It is possible that *N. spathiger* infections are such that only older animals in good condition or with a certain degree of resistance can harbor them without serious consequences.

Because it seemed likely that the parameters of body weight and percent marrow fat were related, both values were plotted for each individual from the collections in 1970-71 in the Kenai (Fig. 2) and at Dry Creek (Fig. 3). Both figures illustrate a general tendency for heavier animals to have more marrow fat, while smaller animals have varied percentages of marrow fat. The clearest relationship is seen among the winter-early spring sheep from the Kenai (Fig. 2), probably because all of these sheep were under uniform conditions of nutritional stress (i.e.

Table 30. 1970-1971 Kenai Peninsula sheep: by marrow fat percent (n=45).

Accession No.	Marrow Fat %	Trichostrongylids
2737	5.8	69
3271	6	1910
3332	15	201
2738	26	12
3331	26	162
3248	28	283
2736	32	155
2735	33	103
3240	38	52
3330	42	46
3263	53	904
3245	57	116
3256	60	496
3242	62	472
3238	65	78
3274	65	195
3254	68	104
3333	71	17
3264	72	94
3276	81	56
3277	82	576
3235	83	63
3267	84	94
3236	85	8
3255	85	90
3244	88	59
3257	88	276
3258	88	446
3259	88	42
3268	88	55
3239	89	618
3262	89	23
3275	89	2
3234	90	311
3249	90	154
3252	90	16
3265	91	23
3250	92	30
3261	92	11
3266	92	442
3273	92	46
3237	93	5
3247	93	21
3270	93	45
3272	94	78
3241	95	2
3251	95	34
3243	96	28
3253	96	120

Table 31. 1972-1973 Dry Creek sheep: marrow fat percentage vs. total mature trichostrongylid burden.

Accession No.*	Marrow Fat %	Total Mature Trichostrongylid
3579	15	3928
3623	37	309
3559	46	749
3580	46	3926
3578	47	981
3697	50	2366
3624	52	714
3581	55	851
3695	63	1572
3696	68	129
3893	87	2762
3868	96	375
3870	96	1384
3894	98	3908
3897	99	1402
3896	99	6724
3895	99	2455

* #3575 omitted because only part of gastrointestinal tract available for examination.

Fig. 2. 1970-1971 Kenai Peninsula sheep: body weight vs. percent marrow fat.

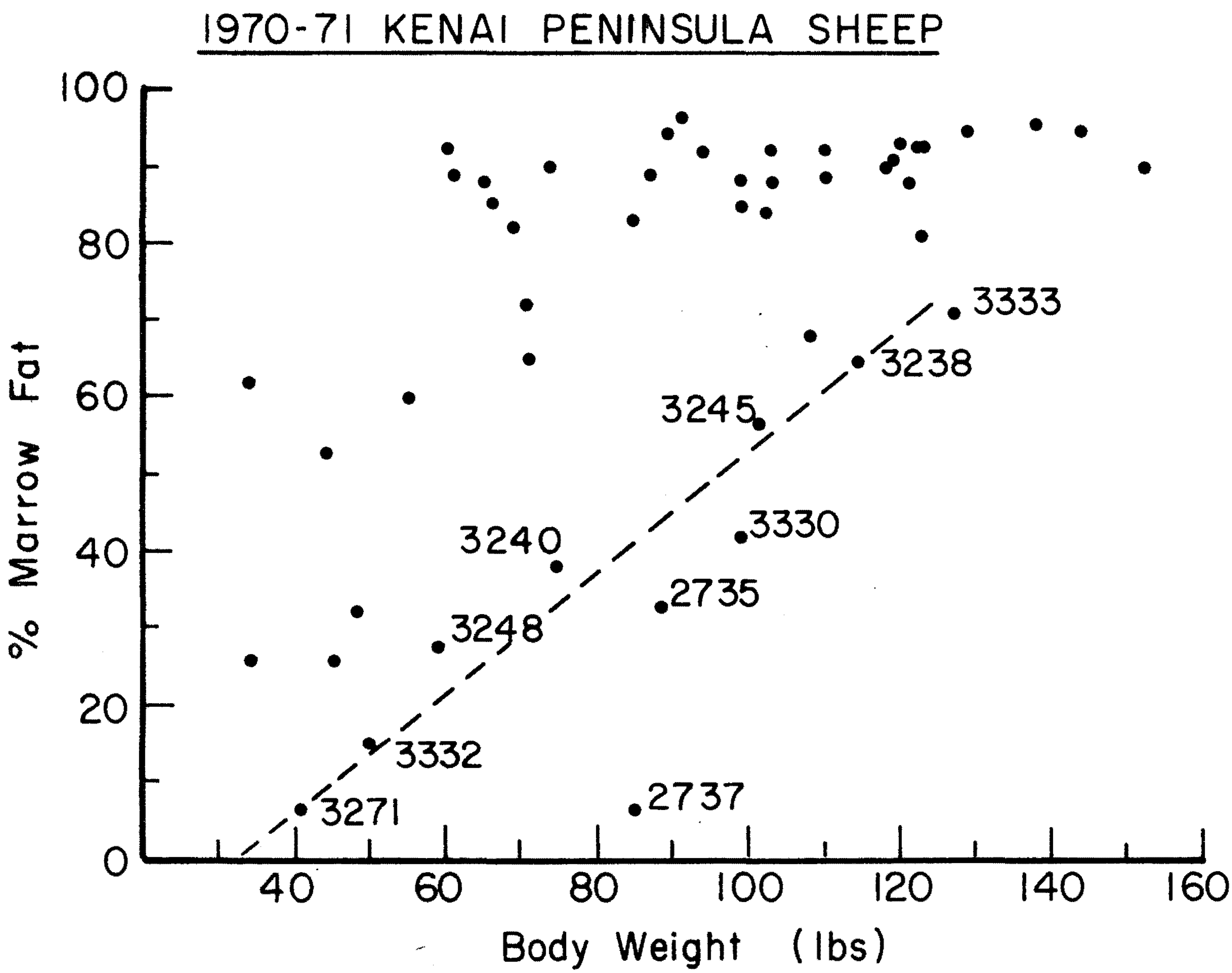
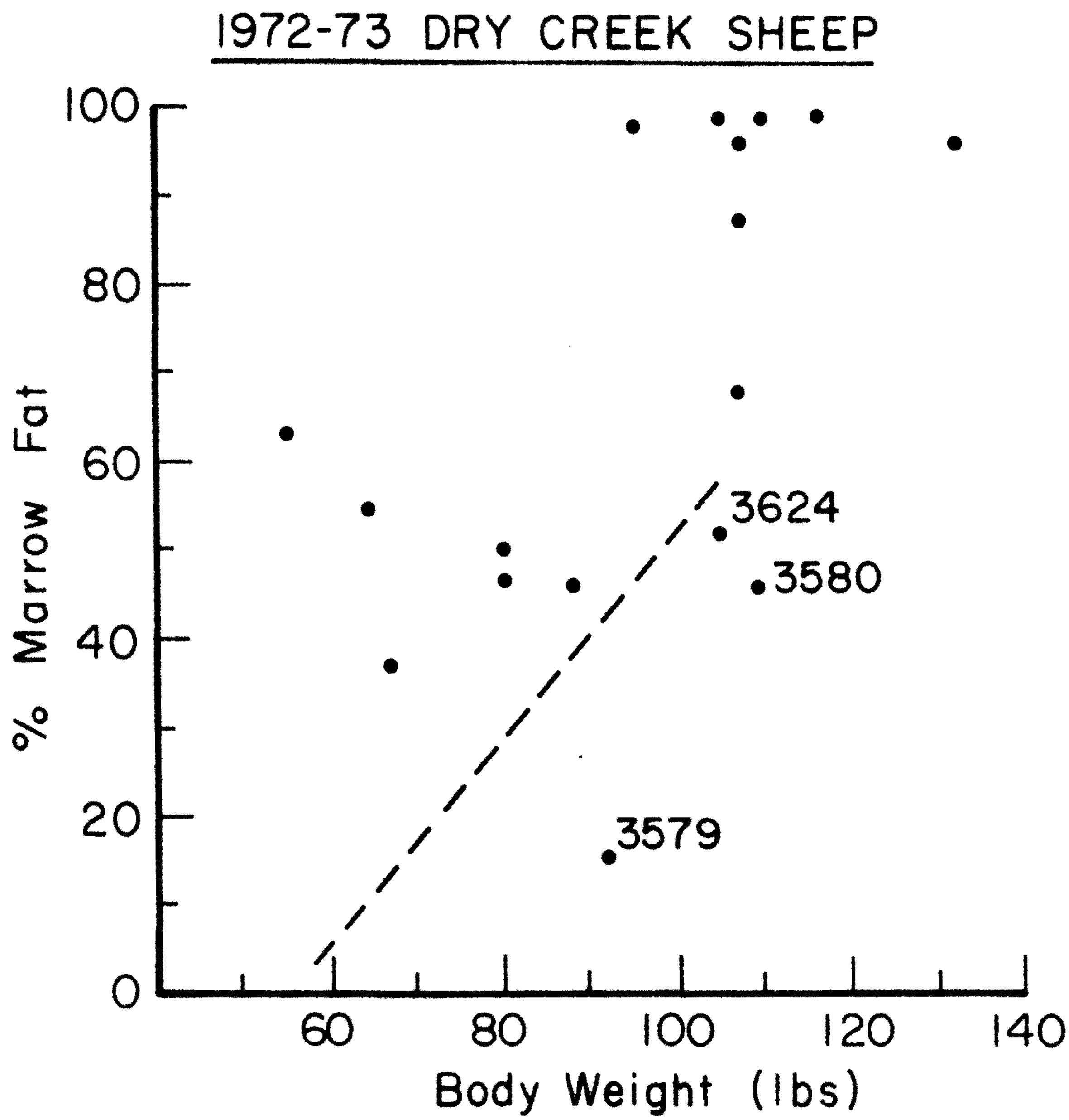


Fig. 3. 1972-73 Dry Creek sheep: body weight vs. percent marrow fat.



decreasing stores of marrow fat). The animals weighing more than 75 pounds tend to have high (80%) marrow fat percentages. Among the 16 sheep weighing less than 75 pounds, 7 had marrow fat percentages between 75 and 92 percent, while the remaining 9 had percentages ranging from 6 to 65 percent. Six of these nine animals were lambs and three were yearlings.

Even among animals weighing more than 75 pounds, several seem to have relatively low marrow fat percentages for their weights. It can be assumed that heavy animals with very low marrow fat percentages (such as the percentages found among some lambs and yearlings) are missing because they have been "selected against." Thus a dotted line was drawn across the graphs to approximate the "danger point" of marrow fat depletion for animals at different weights. The trichostrongylid burdens of the eight sheep from the Kenai and three from Dry Creek which were in the vicinity of this hypothetical "danger line" were examined in detail (Table 32), but no clear differences were seen in either the particular species or numbers of trichostrongylids found when these sheep were compared to all other sheep in those collections. The only possible exception was that the number of *Nematodirus archari* recovered from Dry Creek sheep #3580, a seven-year-old ewe taken in May at Dry Creek, was rather large.

6. Reproductive Condition of the Host

Of the 50 sheep collected on the Kenai Peninsula, 34 were ewes and 16 were rams (Table 33). The average mature trichostrongylid burden among rams was 283, while among ewes it was 140. Among the 13 nonpregnant ewes the average was 143, and it was nearly the same for the 18 pregnant ewes (155). Only three lactating ewes were collected: these harbored 2, 34 and 94 mature trichostrongylids. The above comparisons of averages should be viewed with some reservations, however, for two reasons: 1) most of the "rams" and the "nonpregnant ewes" were in fact lambs and yearlings while all pregnant and lactating ewes were, of course, adults and 2) as discussed in Procedures, the total trichostrongylid burdens were somewhat doubtful for these sheep because of the less precise methods used. Thus, comparisons of total trichostrongylid burdens among various animals from the Kenai Peninsula have inherent uncertainties.

Because the data from Dry Creek are quantitatively more reliable, more meaningful comparisons can be made (Table 34). Only one ram, a yearling, was collected and harbored 1,572 mature trichostrongylids. Sixteen ewes were collected, harboring on the average 1,930 trichostrongylids. The eight nonpregnant ewes had an average trichostrongylid burden of 1,360, while the 6 pregnant ewes averaged 3,118. Two ewes were lactating when collected; they harbored 749 and 129 trichostrongylids. These results indicate that the pregnant ewes were infected, on the average, with more than twice the number of trichostrongylids than nonpregnant ewes. It is interesting to note that in both groups certain individuals were much lower than the average: nonpregnant ewe #3623 harbored only 309 trichostrongylids and pregnant ewe #3624 harbored only 714. Both of these ewes were taken in June 1972.

Table 32. Trichostrongylid infection by species in sheep with low percentage marrow fat in relation to body weight.

	1970-71 Kenai Peninsula									1972 Dry Creek		
Sheep No.	2737	3271	3332	2735	3240	3330	3245	3238	3333	3579	3624	3580
Age & Sex	10 F	3/4M	1 M	7 F	2 M	5 F	5 F	6 F	11 F	7 F	13 F	7 F
Body Weight	85	41	50	88	75	99	101	114	127	92	105	109
% Marrow Fat	5.8	6	15	33	38	42	57	65	71	15	52	46
M. marshalli	9	579	42	29	43	-	54	47	6	704	178	762
O. circumcincta	-	-	1	-	-	-	-	-	-	-	112	3
O. occidentalis	-	12	-	1	-	-	-	-	-	28	6	19
O. ostertagi	-	-	-	-	-	-	-	-	-	-	-	-
O. trifurcata	-	-	-	-	-	-	-	-	-	-	26	4
All *Ost.* spp.	-	12	1	1	-	-	-	-	-	28	144	26
T. davtiani	-	-	-	-	-	-	-	-	-	1	15	2
N. archari	-	74	7	3	9	7	3	14	1	224	20	775
N. davtiani	-	15	6	1	-	-	-	9	2	1	1	19
N. oiratianus	-	64	18	-	-	35	-	1	-	1	1	1
N. spathiger	-	97	2	-	-	-	-	-	-	-	-	69
N. spp. unidentified	-	-	-	-	-	-	-	-	-	-	-	2
All *N.* spp.	-	250	33	4	9	42	3	24	3	226	22	866
Nematodirella spp.	-	-	-	-	-	-	-	-	-	-	-	-
Total Male	9	841	76	34	52	42	57	71	9	959	359	1656
Total Female	60	1069	125	69	-	4	59	7	8	895	355	2270
Total Mature Trichostrongylids	69	1910	201	103	52	46	116	78	17	1854	714	3926

Table 33. 1970-1971 Kenai Peninsula collection: reproductive condition vs. trichostrongylid burden. Total animals = 50 (ewes = 34, rams = 16).

Rams (n=16)		Nonpregnant ewes (n=13)		Pregnant ewes (n=18)		Lactating ewes (n=3)	
No.	Total Trichostrongylids	No.	Total Trichostrongylids	No.	Total Trichostrongylids	No.	Total Trichostrongylids
3236	8	3242	472	3234	311	3241	2
3240	52	3247	21	3235	63	3251	34
3244	59	3253	120	3238	78	3267	94
3248	283	3256	496	3239	618		$\bar{x}$ = 130/3 = 43
3249	154	3262	23	3245	116		
3250	30	3274	195	3254	104		
3252	16	3331	162	3257	276		
3255	90	3237	5	3258	446		
3259	42	3243	28	3261	11		
3263	904	2737	69	3265	23		
3264	94	2736	155	3266	442		
3268	55	2738	12	3269	51		
3271	1910	2735	103	3270	45		
3273	46		$\bar{x}$ = 1861/13 = 143	3272	78		
3277	576			3275	2		
3332	201			3276	56		
	$\bar{x}$ = 4520/16 = 283			3330	46		
				3333	17		
					$\bar{x}$ = 2781/18 = 155		

All ewes, $\bar{x}$ = 4772/34 = 140

Table 34. 1972-1973 Dry Creek sheep: reproductive condition vs. total mature trichostrongylid burden.

Nonpregnant		Pregnant		Lactating	
3578	981	3580	3926	3559	749
3579	1854	3624	714	3696	129
3581	851	3894	3908	n = 2 sheep	
3623	309	3895	2455	all = 878/2 = 439	
3697	2366	3896	6724		
3868	375	3897	1402		
3870	1384	n = 6 ewes			
3893	2762	all = 19,129/6 = 3188			
n = 8 ewes					
all = 10,882/8 = 1360					

When the particular species burdens of the six pregnant and eight nonpregnant ewes from Dry Creek were examined in detail, specific differences between the two groups were noted (Tables 35 and 36). The average numbers of *Teladorsagia davtiani* were similar for both groups, but nonpregnant ewes had nearly three times as many specimens of *Ostertagia* spp., while the pregnant ewes had almost twice the number of *Marshallagia marshalli* and nearly four times as many specimens of *Nematodirus* spp. Unfortunately, a sample bias may have influenced these data. Four of the six pregnant sheep were collected in April 1973, while seven of the eight nonpregnant sheep were collected during 1972, five of these during the spring and summer. Since it has been previously noted that *Ostertagia* appears primarily in the late spring and summer, it is not surprising that the nonpregnant group, five of which were collected at that time, showed more specimens of that genus than the pregnant ewes, four of which were collected in early spring. However, the greater numbers of *Marshallagia* and *Nematodirus* in the pregnant ewes is not so easily explained by sample bias, since this genus occurs commonly into the early summer, well encompassing the time span when the nonpregnant ewes were collected. Of the pregnant ewes, four were collected in April (1973), one in early May and one in early June. The ewes taken in April and May all harbored numerous specimens of *Nematodirus*, but the ewe taken in June harbored very few. These are examples of the "spring rise" phenomenon, particularly the large numbers of *Nematodirus* seen in pregnant ewes.

None of the 50 sheep taken in 1970-71 on the Kenai Peninsula and only 3 of the 18 sheep taken at Dry Creek were collected on mineral licks. This sample size is too small to explain the effect of mineral lick usage on the size of the trichostrongylid burden.

7. Numbers and Locations of Immature Trichostrongylids

Because immature trichostrongylids are small, thin and usually embedded in the crypts of the gastrointestinal mucosa, they are much more difficult to recover than mature specimens. Among domestic animals, immature trichostrongylids are generally recovered from freshly killed sheep by digesting away the mucosa or by simply suspending it in a saline solution and allowing specimens to wriggle free by themselves. However, because of logistic problems all of the wild sheep carcasses in this study were frozen at the collection location or immediately afterward, rendering sophisticated, immature trichostrongylid recovery techniques impossible. Thus immature specimens were generally found only incidentally to the recovery of mature trichostrongylids. Table 37 gives the small number of immatures recovered from the collection in 1970-71 on the Kenai Peninsula and the 1964-73 collections at miscellaneous locations. Table 38 shows the number recovered from sheep taken at Dry Creek in 1972. Only one of the eight sheep from miscellaneous locations, a ten-year-old ram from the Granite Mountains, yielded a few immatures. Immatures, averaging 11 per sheep, were recovered from only 12 of the 50 sheep from the Kenai Peninsula. Of the 12 sheep taken in 1972 in Dry Creek (#3575, a partial tract, was again omitted), immature trichostrongylids were recovered from 9 animals, averaging 29 per sheep.

Table 35. 1972-1973 Dry Creek sheep: reproductive condition vs. trichostrongylid burden by species.

	Pregnant Ewes								Lactating Ewes	
	3580 7 F 5/5/72	3624 13 F 6/5/72	3894 2 F 4/10/73	3895 7 F 4/10/73	3896 8 F 4/10/73	3897 5 F 4/10/73	Total	Preg. n = 6 $\bar{x}$	3559 4 F 3/18/72	3696 11 F 7/9/72
Mature Males										
M. marshalli	762	178	391	557	2027	210	4125	688	173	7
O. circumcincta	3	112	-	-	-	-	115	58	-	20
O. occidentalis	19	6	15	5	22	-	67	11	4	2
O. ostertagi	-	-	-	-	-	-	-	-	-	-
O. trifurcata	4	26	-	-	-	-	30	5	-	4
All *Ostertagia* spp.	26	144	15	5	22	-	212	35	4	26
T. davtiani	2	15	-	-	-	-	17	3	-	2
N. archari	775	20	1180	275	760	155	3165	528	7	-
N. davtiani	19	1	214	12	148	96	490	82	-	-
N. oiratianus	1	1	35	11	-	-	48	8	-	-
N. spathiger	69	-	410	365	242	431	1517	253	-	4
N. spp. unidentified	2	-	-	-	-	-	2	-	-	-
All *Nematodirus* spp.	866	22	1839	663	1150	682	5227	871	7	4
Nematodirella spp.	-	-	7	121	-	-	128		-	-
Total Males	1656	359	2252	1346	3199	892	9704	1617	184	39
Total All Females	2270	355	1656	1109	3525	510	9425	1571	565	90
Total Mature Trichostrongylids	3926	714	3908	2455	6724	1402	19,129	3188	749	129

Table 36. 1972-1973 Dry Creek sheep: reproductive condition vs. trichostrongylid burden by species.

	Nonpregnant Ewes									Non-preg.	Ram
	3578 4 F 5/5/72	3579 7 F 5/5/72	3581 1 F 5/4/72	3623 1 F 6/5/72	3697 4 F 7/9/72	3868 3 F 11/17/72	3870 5 F 11/17/72	3893 8 F 4/10/73	Total	n = 8 $\bar{x}$	3695 1 M 7/9/72
Mature Males											
M. marshalli	455	704	281	51	227	184	301	565	2768	346	485
O. circumcincta	2	-	1	46	602	-	-	-	651	81	81
O. occidentalis	10	28	15	10	52	1	8	-	124	16	42
O. ostertagi	-	-	-	-	-	-	-	-	-	-	22
O. trifurcata	3	-	-	11	79	-	-	-	93	12	17
All *Ostertagia* spp.	15	28	16	67	733	1	8	-	868	109	162
T. davtiani	-	1	-	9	28	-	-	-	38	5	6
N. archari	27	224	60	4	141	-	100	715	1271	159	7
N. davtiani	2	1	7	3	23	-	32	2	70	9	-
N. oiratianus	1	1	57	15	110	-	36	5	225	28	5
N. spathiger	-	-	-	-	17	-	202	85	304	38	2
N. spp. unidentified	1	-	-	-	2	-	-	-	3	-	-
All *Nematodirus* spp.	31	226	124	22	293	-	370	807	1873	234	14
Nematodirella spp.	-	-	-	-	-	-	-	-	-	-	-
Total Males	501	959	421	149	1281	185	679	1372	5547	693	667
Total All Females	480	895	430	160	1085	190	705	1390	-	-	905
Total Mature Trichostrongylids	981	1854	851	309	2366	375	1384	2762	-	-	1572

Table 37. Total number of immature trichostrongylid specimens recovered from the Kenai Peninsula and miscellaneous locations.

	Acc. No.	Date	Age	Sex	Total Immature Trichostrongylids
1970-1971 Kenai Peninsula Collection	2737	4/28/70	10	F	10
	2738	4/28/70	2	F	1
	3234	2/26/71	9 1/2	F	20
	3235	2/26/71	2 1/2	F	10
	3239	2/26/71	2 3/4	F	25
	3242	4/27/71	1	F	5
	3245	4/27/71	5	F	3
	3248	1/27/71	2	M	10
	3263	3/18/71	3/4	M	20
	3271	3/18/71	3/4	M	20
	3276	2/26/71	13 1/2	F	1
	3277	3/18/71	1 3/4	M	5
1964-1973 Miscellaneous Location Collection	3339	8/11/71	10	M	5
	Total = 13 sheep $\bar{x}$ = 10				135
	Total Kenai Collection = 12 sheep, 130 immatures $\bar{x}$ = 11				

Table 38. Total number of immature trichostrongylids recovered from 1972 Dry Creek sheep.

Acc. No.	Date	Age	Sex	Total Immature Trichostrongylids
3559	3/18/72	4	F	29
3578	5/5/72	4	F	8
3579	5/5/72	7	F	35
3580	5/5/72	7	F	105
3624	6/5/72	13	F	5
3695	7/9/72	1	M	41
3697	7/9/72	4	F	16
3868	11/17/72	3	F	15
3870	11/17/72	5	F	5
Total = 9 sheep, $\bar{x}$ = 29				259

A concerted effort was made to establish the number of immature trichostrongylids more precisely for the sheep taken in 1973 at Dry Creek. This was done at least partly because it was obvious upon preliminary examination that there were many immatures in all five animals collected in April. In the first sheep examined (#3896, an eight-year-old ewe), specimens of what appeared to be fourth and early fifth stage larvae were seen in very large numbers in the duodenum and anterior part of the small intestine. Numerous specimens were collected and a rough estimate of the total number present was made (Table 39). More precise information was available for the remaining four sheep. In these, 20 percent of the gut was sampled and subsamples were made to accurately estimate the numbers of immatures present in each section of the tract.

In these 5 sheep, 93 percent of the total immatures found were located in the anterior half of the small intestine, 2 percent in the abomasum, 4 percent in the duodenum, and a negligible number in the posterior small intestine, caecum and colon. For the 3 sheep in which the anterior half of the small intestine was again divided in half, 96 percent of the total immature trichostrongylids were in the first 4 meters of the small intestine. In 2 sheep, this section of the intestine was further subdivided into 4 equal parts, and 93 percent of the total immatures found in each sheep were located in the first 2 meters of this part of the gut (AS1 and AS2).

The time of year (April) of this collection probably had a considerable influence on the locations in which immature trichostrongylids were found. As discussed earlier, species of *Nematodirus*, the primary inhabitants of the small intestine, begin to increase in the early spring, particularly in pregnant sheep (four of these animals were pregnant; the nonpregnant ewe had the smallest number of immatures). Therefore, it is suspected the large numbers of intestinal immatures, as seen in seven-year-old ewe #3895 and eight-year-old ewe #3896, represented the early stages of an increase in species of *Nematodirus*. Therefore one would expect to see an increase in abomasal immatures just prior to the late "spring rise" in species of *Ostertagia*. Indeed, some immature specimens were encountered in three of the four ewes collected in early May of 1972 at Dry Creek (Table 38) although for these sheep immature specimens were collected only sporadically.

For two of the sheep taken at Dry Creek in 1973, the abomasum was divided into its cardiac-fundic and pyloric portions. In sheep #3894 all 225 abomasal immatures were found in the pyloric section, while for sheep #3895, 81 percent (305/375) were in the pyloric section and the remaining immatures were in the cardiac-fundus.

The largest number of immatures seen in a single animal was the nearly 25,000 found in a seven-year-old 1973 Dry Creek ewe. Of this total, 98 percent (24,200/24,785) were in "anterior small intestine A;" and 89 percent (22,000/24,785) were within the second meter of this region.

Table 39. 1973 Dry Creek sheep: numbers and locations of immature trichostrongylids.

Sheep No.	Total Immatures	Abo	Duod	As 1	As 2	As 3	As 4	Ant. Sm. A	Jeju	Ant. Sm. Intestine	Post. Sm.	Caecum & Colon
3893	970	60	105					800	5		-	-
3894	2575	225	145	1400	395	245	75	2115	85		5	-
3895	24,785	375	160	1725	22,000	325	150	24,200	35		15	-
3896	14,534	100	1400							13,000	34	-
3897	1265	235	125							760	45	100
n = 5	44,129	995 (2%)	1935 (4%)	n=2 3125 (11%)	n=2 22,395 (82%)	n=2 570 (2%)	n=2 225 (1%)	n=3 27,115 (96%)	n=3 125 (1/2%)	n=5 41,000 (93%)	99 (<1%)	100 (<1%)

A rapid survey of some of the immature specimens found indicated nearly all were late fourth and early fifth stage larvae. Immature male specimens were not infrequently found which could be classified to genus but not to species. These specimens were classified as "immatures." Usually this situation involved lack of definitive spicule sclerotization or, for the Ostertagiinae, lack of genital cone development.

B. Pinworms

Pinworms, small oxyurid nematodes of the genus *Skrjabinema* Vereshchagin, 1926, are inhabitants of the lower digestive tract of many mammals. They were encountered in 10 of the 53 sheep collected on the Kenai Peninsula in 1970-71 (Table 40). However, no concerted effort was made to find *Skrjabinema* when these sheep were examined; those few specimens recovered were randomly encountered while personnel quickly searched for whipworms. Since the total number of *Skrjabinema*, particularly male specimens, can be determined only by diligently searching through the bulky contents of the lower digestive tract (or of a volumetric sample), data on the prevelance and numbers of *Skrjabinema* found in sheep from the Kenai Peninsula are not accurate. The same inaccuracy probably applies to seven of the eight sheep taken at "miscellaneous locations." Several *Skrjabinema* specimens were found in one of these sheep, a 9-year-old ram from the Granite Mountains. The eighth sheep, a 6-week-old lamb from the Tok River area, was carefully examined for *Skrjabinema* and yielded 70 specimens (caecum:58, colon:12).

The numbers, locations and sexes of *Skrjabinema* recovered from 11 of the 13 sheep taken at Dry Creek in 1972 (pinworms were not noticed in the first two sheep examined, #3559 and #3575) were given in Table III of Ericson and Neiland's 1973 report. The total recovered from these 11 animals was 4,670 *Skrjabinema* (range 2-2390). Numbers, locations and sexes of pinworms recovered from the five sheep taken at Dry Creek in 1973 are given in Table 41. The total recovered from these five sheep was 8,532 *Skrjabinema* (range 435 - 4,561).

It is apparent that many more pinworms were recovered from the sheep taken in 1973 than from animals collected in 1972. Since there was no further refinement of the technique, it is felt this difference represented the actual situation. Careful examination of the data collected in 1972 indicates that the two sheep collected in November had the fewest *Skrjabinema*. The two pregnant ewes had the largest and third largest number of pinworms. The smallest number of pinworms (55) was encountered in a yearling male; the other yearling, a female, had an average number (360) of *Skrjabinema*. Among the sheep taken in 1973, the nonpregnant ewe (an 8-year-old) had the lowest number of pinworms (435). The most pinworms found in any of the sheep examined was 4,561 from the other 8-year-old ewe taken in April 1973. It appears that there is both seasonal and individual variation in numbers of *Skrjabinema*, and that pregnant ewes tend to have more of these nematodes.

Among the total *Skrjabinema* found in 1972 in sheep taken at Dry Creek, less than 1 percent (25/4670) were in the small intestine, 80 percent (3727/4670) were in the caecum and 20 percent (921/4670) were in

Table 40. 1970-1971 Kenai Peninsula sheep: *Skrjabinema* and *Trichuris*.

Ovis dalli				*Skrjabinema* spp.			*Trichuris* spp.		
Acc. No.	Date	Age	Sex	Total	Small Int.	Caecum	Total	Small Int.	Caecum
3244	11/13/70	1/2	M	10	-	10	-	-	-
3250	11/13/70	1/2	M	-	-	-	-	-	-
3252	11/13/70	1/2	M	6	-	6	-	-	-
3255	1/14/71	1/2	M	-	-	-	-	-	-
3262	1/14/71	1/2	F	-	-	-	-	-	-
3256	3/18/71	3/4	F	-	-	-	-	-	-
3263	3/18/71	3/4	M	-	-	-	-	-	-
3271	3/18/71	3/4	M	-	-	-	6	-	6
3331	4/27/71	1	F	-	-	-	94	-	94
3332	4/27/71	1	M	2	2	-	22	-	22
3242	4/27/71	1	F	-	-	-	150	-	150
n = 11				18	2	16	272	-	272
3259	1/14/71	1 1/2	M	-	-	-	-	-	-
3273	1/14/71	1 1/2	M	-	-	-	-	-	-
3236	2/26/71	1 1/2	M	-	-	-	-	-	-
3275	2/26/71	1 3/4	F	-	-	-	-	-	-
3264	3/18/71	1 3/4	M	-	-	-	25	-	25
3272	3/18/71	1 3/4	F	-	-	-	-	-	-
3274	3/18/71	1 3/4	F	-	-	-	3	-	3
3277	3/18/71	1 3/4	M	-	-	-	-	-	-
2736	4/28/70	2	F	-	-	-	-	-	-
2738	4/28/70	2	F	-	-	-	-	-	-
2739	4/28/70	2	F	-	-	-	2	-	2
3240	4/27/71	2	M	-	-	-	16	-	16
3248	4/27/71	2	M	1	-	1	2	-	2
n = 13				1	-	1	48	-	48
3247	11/13/70	2 1/2	F	-	-	-	-	-	-
3253	11/13/70	2 1/2	F	-	-	-	-	-	-
3251	11/13/70	3 1/2	F	-	-	-	-	-	-
3269	1/14/71	3 1/2	F	-	-	-	-	-	-
3235	2/26/71	2 1/2	F	-	-	-	-	-	-
3239	2/26/71	2 3/4	F	-	-	-	-	-	-
3268	2/26/71	2 3/4	M	3	-	3	-	-	-
3249	2/26/71	3 3/4	M	22	-	22	-	-	-
3266	3/18/71	3 3/4	F	-	-	-	-	-	-
n = 9				25	-	25	-	-	-
3237	11/13/70	6 1/2	F	-	-	-	-	-	-
3241	11/13/70	7 1/2	F	-	-	-	1	-	1
3270	1/14/71	6 1/2	F	-	-	-	-	-	-
3246	2/26/71	5 3/4	F	-	-	-	6	-	6
3261	2/26/71	6 3/4	F	-	-	-	-	-	-

Table 40. Continued.

Ovis dalli				*Skrjabinema* spp.			*Trichuris* spp.		
Acc. No.	Date	Age	Sex	Total	Small Int.	Caecum	Total	Small Int.	Caecum
3258	3/18/71	5 3/4	F	-	-	-	4	-	4
3257	3/18/71	7+	F	-	-	-	-	-	-
3330	4/27/71	5	F	5	-	5	-	-	-
3245	4/27/71	5	F	49	4	45	5	-	5
3238	4/27/71	6	F	-	-	-	-	-	-
2735	4/28/70	7	F	-	-	-	-	-	-
n = 11				54	4	50	16	-	16
3243	11/13/70	8 1/2	F	-	-	-	-	-	-
3267	1/14/71	8 1/2	F	-	-	-	-	-	-
3234	2/26/71	9 1/2	F	2	-	2	-	-	-
3276	2/26/71	13 1/2	F	2	-	2	-	-	-
3265	3/18/71	9 3/4	F	-	-	-	-	-	-
3254	3/18/71	10 3/4	F	-	-	-	-	-	-
2737	4/28/70	10	F	-	-	-	-	-	-
3333	4/27/71	11	F	-	-	-	-	-	-
3233	4/27/71	14	F	-	-	-	-	-	-
n = 9				4	-	4	-	-	-
Total:				102	6	96	336	-	336
n = 53				n = 10			n = 13		

Table 41. *Skrjabinema* recovered from Dry Creek sheep taken April 10, 1973.

Acc. No.	Age	Sex	*Skrjabinema* Small Intestine M	F	Total	Caecum M	F	Total	Colon M	F	Total	Total M	F	Total	Reproductive Condition
3893	8	F	–	–	–	75	50	125	260	50	310	335	100	435	nonpregnant
3894	2	F	–	–	–	410	420	830	275	275	550	685	695	1380	pregnant
3895	7	F	–	5	5	170	275	445	420	310	730	590	590	1180	pregnant
3896	8	F	–	–	–	1744	2378	4122	190	249	439	1934	2627	4561	pregnant
3897	5	F	–	–	–	200	625	825	1	150	151	201	775	976	pregnant
n = 5 sheep			–	5	5 (<1%)	2599	3748	6347 (74%)	1146	1034	2180 (26%)	3745	4787	8532	

the colon. Locations were similar for the sheep collected in 1973. Less than 1 percent (5/8532) were in the small intestine, 74 percent (6347/8532) were in the caecum and 26 percent (2180/8532) were in the colon. The colon of the sheep with the largest number of *Skrjabinema* was divided in half (not including the posterior area where soft, formed pellets were present). In this instance, 85 percent (373/439) of the *Skrjabinema* found in the colon were in the anterior half, while the remainder (66/439) were in the posterior part. Thus it appears that nearly all *Skrjabinema* exist in the caecum and anterior colon.

The numerous *Skrjabinema* specimens found have not yet been identified to species.

C. Whipworms

Whipworms are medium-sized nematodes belonging to the genus *Trichuris* Roederer, 1761. They, like pinworms, are primarily parasites of the caecum and colon. Whipworms were frequently encountered in the sheep examined, but the infections only rarely consisted of more than a few specimens per sheep. None of the eight sheep taken at miscellaneous locations harbored whipworms. Of the 53 sheep taken on the Kenai in 1970 and 1971, 25 percent (13/53) had *Trichuris* infections ranging from 1 to approximately 150 specimens (Table 40). The larger infections (22, 94, 150) were encountered among nearly-year-old lambs taken in April. Yearlings taken in March and April had moderate infections (range 2-25). Sheep two years old and older generally had few *Trichuris* (range 1-6). Of the 336 total whipworms found in sheep taken on the Kenai in 1970-71, 81 percent (272/336) were found in lambs, and 98 percent (329/336) were found in animals collected in March and April.

Eleven of the 13 sheep collected at Dry Creek in 1972 harbored *Trichuris* spp. (Table IV of Ericson and Neiland 1973), with infections ranging from 2 to 44 specimens per sheep. The larger infections (28, 36 and 44 specimens) were encountered in May and July, with the two largest infections found in yearlings. Among the five animals taken in 1973 at Dry Creek, all collected in early April (i.e. three sheep) harbored *Trichuris* spp. (Table 42). The youngest animal of the five, a two-year-old, harbored the most specimens of *Trichuris* (i.e. 15).

Of particular interest among the animals taken at Dry Creek in 1972 and 1973 was the observation that in some animals the caecal mucosa, and in some cases the mucosa of the anterior colon, was dotted with small nodules. These round nodules ranged in size from two to seven mm in diameter and were elevated from one to three mm above the mucosa. When examined by Drs. R. L. Rausch (of the Arctic Health Research Center, Fairbanks) and R. Van Pelt (of the Institute of Arctic Biology, Fairbanks), these nodules appeared to be filled with leucocytes and unrecognizable necrotic material. Since *Trichuris* spp. develop to the adult stage in the mucosa, it is possible that these nodules are associated with an immune response by the host to developing *Trichuris*. Accordingly, when nodule density is compared with number of *Trichuris* individuals found, they appear to be inversely related in four of the five sheep, as would

Table 42. 1973 Dry Creek sheep: number and location of *Trichuris* spp.

				Trichuris spp.		
Acc. No.	Date	Age	Sex	Total	Location	Nodules in Caecal Mucosa
3893	4/10/73	8	F	-	-	many
3894	4/10/73	2	F	15	caecum & colon	some
3895	4/10/73	7	F	10	caecum: 5	moderate
3896	4/10/73	8	F	-	-	some
3897	4/10/73	5	F	2	caecum	very many
Total n = 5				27		

be consistent with immune response. Two of the sheep taken at Dry Creek in 1972 displayed some caecal nodules: #3579, a 7-year-old ewe taken in early May with 4 *Trichuris*, had a few nodules and #3870, a 5-year-old ewe taken in mid-November with 3 *Trichuris*, had some nodules.

As yet, the species of *Trichuris* present in sheep on the Kenai and at Dry Creek has not been determined.

D. Other Infections

A total of 18 sheep were examined for lump jaw, of which 4 were positive. A 5-year-old ram from the Wood River area and a 10-year-old ram from the Alaska Range west of Farewell had lump jaw infections. Two ewes from Dry Creek (April 1973) were positive: #3893, an 8-year-old, had large lumps on the rami of both jaws, several molars were missing, but no sulfur granules were evident in the porous reactive lesion tissue; #3895, a 7-year-old, had a fenestration on the right mandible, and one molar was missing. The jaw from the latter animal was sent to Dr. Lucille Georg at the Center for Disease Control in Atlanta for further study, but her report on this case has not yet been received.

Lungs were collected from the 10 sheep taken in April 1973 (5 from the Dry Creek collection and 5 from the Granite Mts.), and from one 6-week-old female lamb found dead in the Tok River area. These specimens have been frozen and await examination for lungworm infection.

Fecal pellet samples were recovered from a group of six individuals in the White Mountains and from another group of 10 sheep in the upper Noatak River area. Pellets were also recovered from an adult ram in the Noatak area, and directly from the rectum of the 10 Dry Creek and Granite Mountains sheep. All of these pellet specimens have yet to be examined for nematode eggs, coccidia and lungworm larvae.

DISCUSSION

A. Gastrointestinal Nematodes of *Ovis dalli*

Gastrointestinal nematodes have been examined for six species of wild *Ovis* (excluding animals held in zoos): *O. canadensis*, *O. nivicola*, *O. ammon*, *O. ophion*, *O. vignei* and *O. musimon*. Of the 14 species (7 genera) of nematodes reported here for *O. dalli*, 13 have been found also in *O. canadensis*, 3 in *O. nivicola*, 13 in *O. ammon*, 7 in the urials (*O. vignei* and *O. ophion*), and 8 in *O. musimon* (see Appendix).

According to Cowan (1940) and Geist (1971), *O. dalli* is most closely related to *O. canadensis*. Many Russian investigators, including Cherniavski (1962) and Flerov (1967) consider *O. dalli* to be conspecific with the Siberian snow sheep *O. nivicola* on the basis of morphology. However, recent chromosomal studies by Vorontsov and Liapunova (1973) and Rausch (personal communication) have substantiated a closer relationship between

O. dalli and *O. canadensis*. Indeed the gastrointestinal parasite faunas in these two species are very similar, although *O. canadensis* harbors a variety of species not seen in *O. dalli*, probably because the former is frequently in contact with domestic livestock. Unfortunately there has been only a single study of the gastrointestinal parasites of *O. nivicola*, in which Gubanov (1964) found four of the more abundant species found in *O. dalli*. *Ovis ammon*, more distantly related to *O. dalli*, has nevertheless a fauna very similar to it. Like *O. canadensis*, *O. ammon* frequently harbors species of parasites probably acquired from domestic livestock. *Ovis ophion* and *O. vignei* have been little studied, but are known to harbor some of the species found in *O. dalli*. *Ovis orientalis*, a distant relative, has not been examined at all. *Ovis musimon*, phylogenetically the most distantly removed from *O. dalli*, has about half the species found in the latter plus a great variety of other species probably due to its frequent and long-established contact with domestic stock. Thus differences in climate and faunal environment tend to obscure whatever relationships exist between ovid phylogeny and the species composition of gastrointestinal parasites harbored by sheep.

We are aware of only two reports of gastrointestinal nematodes from *O. dalli* aside from the present work. R. L. Rausch (personal communication) obtained trichostrongylids from the abomasum of two Dall sheep from the Brooks Range, which W. W. Becklund identified as *Marshallagia marshalli* and *Ostertagia occidentalis*. N. Simmons (personal communication), of the Canadian Wildlife Service, examined 21 Dall sheep from the Mackenzie Mountains (NWT) and found *M. marshalli*, *Nematodirus* spp., *Skrjabinema ovis*, *Trichuris* sp., and *Capillaria* sp. Both of these observations are in agreement with our findings, with the exception that Simmons encountered three specimens of *Capillaria* sp. in the caecum of one of the 21 sheep examined, while we did not encounter this species at all. *Capillaria* is apparently a very infrequent parasite of wild *Ovis*. The genus was reported from *O. canadensis* in Alberta (2 specimens were found in 1 of 25 sheep, a diseased lamb) by Uhazy and Holmes (1971) and *C. bovis* has been reported in *O. musimon* in Czechoslovakia (Kotrly 1967), Austria (Kutzer and Hinaidy 1969), and Germany (Boch and Horchner 1962). *Capillaria* occurs "generally in North America" among domestic sheep (Becklund 1964).

A list of the species found in *O. dalli* in the present study, together with a discussion of their occurrence in other wild *Ovis* species is given below.

1. *Marshallagia marshalli*

Marshallagia marshalli was the most prevalent and most abundant trichostrongylid found in *O. dalli*. It has been seen frequently in *O. canadensis* in Alberta and British Columbia (Cowan 1951, Blood 1963, Uhazy and Holmes 1971), Idaho (Quodrup and Sudheimer 1944), Montana (Rush 1932, Dikmans 1932, Mills 1937, Marsh 1938, Couey 1950, Becklund and Senger 1967), Wyoming (Honess and Winter 1956), Colorado (Spencer 1943) and South Dakota (Boddicker and Hugghins 1969). It has also been seen in *O. ammon* and *O. ophion* in the USSR (Boev et al. 1963). *Marshallagia mongolica*, a species very similar to *M. marshalli* but distinguished by a weakly chitinized gubernaculum "in a majority of cases" (Skrjabin et al. 1954), has been reported from *O. ophion* and *O. ammon* in Mongolia and the USSR, and *O. nivicola* in Yakutia. Interestingly, only Boev et al. (1963) recorded the genus in *O. musimon* in the USSR. Kutzer and Hinaidy (1969) found *M. marshalli* in the chamois (*Rupicapra rupicapra*) but not in *O. musimon* in Austria. Dikmans (1932) suspected that *M. marshalli* was originally introduced to domestic sheep by wild ungulates in the northwestern U.S., but subsequent findings of *M. marshalli* in domestic sheep worldwide have cast doubt upon this view, although in North America the species does occur almost exclusively in the Rocky Mountains area.

The prevalence and abundance of *M. marshalli* in North American wild sheep, including *O. dalli* which have not had contact with domestic sheep, indicate this species is a "natural" (not acquired) parasite of wild *Ovis* in North America. It is interesting that Becklund and Senger (1967) found numerous *M. marshalli* in *O. canadensis* at Wildhorse Island and Sun River (Montana), but that it was totally absent (supplanted? see Uhazy and Holmes 1971, and below) in wild sheep in the National Bison Range. *Marshallagia* has not been encountered among the desert bighorns of the southwestern U.S., so that this genus, like *Ostertagia* to which it is similar, probably prefers temperate and subarctic conditions.

Total numbers of *M. marshalli* in wild *Ovis* have been counted only twice prior to this study. Becklund and Senger (1967) reported a range of 10-1040 male and female *M. marshalli* ($\bar{x}$ = 475) for four *O. canadensis* in Montana. Uhazy and Holmes (1971) reported 1-382 male *M. marshalli* ($\bar{x}$= 145) for 24 of the same host in Alberta and British Columbia. Gubanov reported 1-382 *M. mongolica* (male and female?; $\bar{x}$ = 113) for 10 *O. nivicola* in Yakutia. In this study the range was 1-2027 male *M. marshalli* ($\bar{x}$ = 317 [1972] and 749 [1973])for carefully examined sheep, which is consistent with the previous findings. Since very little is known about the pathogenesis of *M. marshalli*, it is difficult to determine what affect these burdens have on the sheep.

2. *Ostertagia circumcincta*

Levine (1968) considered *Ostertagia circumcincta* the most important species of *Ostertagia* in domestic sheep, and indeed this nematode is a common and often serious problem among *O. aries* worldwide. It has been reported from nearly all wild *Ovis* species: *O. canadensis* in western Canada (Cowan 1951, Blood 1963, Uhazy and Holmes 1971), Montana (Becklund and Senger 1967) and Wyoming (Honess and Winter 1956); *O. ammon* in Kazakhstan and Turkmenia (Boev et al. 1963, Kibakin et al. 1964); *O. ophion* (Boev et al. 1963); and *O. musimon* in Czechoslovakia (Kotrly 1967), Austria (Kutzer and Hinaidy 1969), Germany (Boch and Horchner 1962) and the Crimea (Roukhladev, in Ianouchko, 1955). As with *M. marshalli*, Becklund and Senger (1967) found *O. circumcincta* among wild sheep on Wildhorse Island but not in 12 sheep from the National Bison Range.

O. circumcincta was seen infrequently (12%) in the *O. dalli* examined during this study. Nine Dall sheep harbored the species but only five sheep (all from the 1972 Dry Creek collection) harbored more than a few male specimens (20, 46, 81, 112 and 602 specimens). Uhazy and Holmes (1971) found *O. circumcincta* in only 3 of 24 *O. canadensis* in Alberta and British Columbia, with a range of 10-60 male and female specimens ($\bar{x}$ = 19). Becklund and Senger (1967) found *O. circumcincta* in 3 of 5

Wildhorse Island sheep, with 10 (male) specimens found in each sheep. Thus it appears that *O. circumcincta* is only an occasional parasite of wild *Ovis*, and that it occurs in high intensities only rarely. Interestingly, the only intense infection (n = 602) reported for wild *Ovis* is the one for *O. dalli* in the present work.

3. *Ostertagia occidentalis*

Ostertagia occidentalis has been widely reported from wild sheep: *O. canadensis* in western Canada (Cowan 1951, Blood 1963, Uhazy and Holmes 1971), Montana (Couey 1951, Becklund and Senger 1967), Wyoming (Honess and Winter 1956), Idaho (Dikmans 1942, Quortrup and Sudheimer 1944) and South Dakota (Boddecker and Hugghins 1969); also *O. ammon* in the USSR (Boev et al. 1963); *O. ophion* in the USSR (Boev et al. 1963); and wild sheep (presumably *O. musimon*) in the Crimea (Roukhladev, in Ianouchko, 1955). Most investigators have found this species to be very prevalent among sheep; Uhazy and Holmes (1971) found it in 21 of 24 sheep, Blood (1963) found it in 2 of 2 sheep, Becklund and Senger (1967) found it in 3 of 5 sheep, Couey (1951) found this species in 4 of 4 sheep, and Boddicker and Hugghins (1969) found it in 3 of 3 sheep. Prior to the present study, however, only two investigators have actually counted the number of specimens present, and in both cases the number was relatively small. Becklund and Senger (1967) counted 10 and 20 specimens, and Uhazy and Holmes (1971) counted an average of 25 specimens (range 2-240). This is in agreement with our findings for *O. dalli*. We found 15 of the 17 carefully examined sheep from Dry Creek infected with an average of 16 male *O. occidentalis* (range 1-52). It appears that *O. occidentalis* is a common trichostrongylid of worldwide distribution which, for some reason, rarely occurs in large numbers. This species was apparently "supplanted" in *O. canadensis* at the National Bison Range (Becklund and Senger 1967). Like *M. marshalli*, in North American domestic sheep *O. occidentalis* occurs primarily in the West (Becklund 1964).

4. *Ostertagia ostertagi*

Ostertagia ostertagi is primarily a parasite of cattle. Although it has been reported in sheep, *Ovis* spp. are apparently somewhat resistant to this species (Herlich and Stewart 1954, Pandey 1971). Previous reports of this species from wild *Ovis* have been in areas where contact exists between wild sheep and domestic cattle: *Ovis canadensis* in southern British Columbia (Blood 1963) and Idaho (Dikmans 1942 and Quortrup and Sudheimer 1944 - both papers erroneously identified *Ostertagia ostertagi* as *Ostertagia gruhneri*, which was corrected by Becklund and Senger 1967); *Ovis ammon* in the USSR (Boev et al. 1963); and *Ovis musimon* in Germany (Boch and Horchner 1962) and the USSR (Boev et al. 1963). Uhazy and Holmes (1971) failed to find *Ostertagia ostertagi* among 24 wild bighorns in Alberta and British Columbia. It is, therefore, interesting that *O. ostertagi* was found in Alaskan Dall sheep, which have had no contact with domestic cattle. The occurrence in Dall sheep was very low, however: 2 sheep of 74 examined harbored 2 and 22 male specimens, respectively. One of the infected sheep was from Dry Creek and one from the Granite Mountains. Although a number of bison were introduced in the area of Delta Junction and range between the Granite Mountains and the Dry Creek foothills, they rarely come into contact with wild sheep range in the area. It is possible, however, considering the very low incidence of *O. ostertagi* in sheep, that these bison did serve as the source of infection. Becklund and Senger's (1967) finding of *O. ostertagi* in 9 of 12 sheep on the National Bison Range, Montana, but in none of 6 bighorns from other areas would support this idea. It therefore appears that *O. ostertagi* may be a parasite of wild sheep only where a reservoir of infection (cattle or bison) is available.

5. *Ostertagia trifurcata*

Ostertagia trifurcata, a common parasite of domestic sheep, has only occasionally been reported from wild *Ovis*. Becklund and Senger (1967) identified one specimen of *O. trifurcata* from Rocky Mountain bighorns in Montana, and Honess and Winter (1956) reported this species from the same host in Wyoming. The species has also been reported from *Ovis ammon* in the USSR (Boev et al. 1963), *O. vignei* in Kazakhkstan (Boev, Lavrov and coworkers 1957, as cited by Gvozdev 1968), and *O. musimon* in Germany (Boch and Horchner 1962), Czechoslovakia (Kotrly 1967), Crimea (Roukhladev, in Ianouchko 1955), and the USSR (Boev et al. 1963). In Dall sheep *Ostertagia trifurcata* was found in only 8 of the 74 sheep examined in this study, always in small numbers ($\bar{x}$ = 18 males, range 1-79), and usually together with other species of *Ostertagia*. All of these eight sheep were taken at Dry Creek. It appears that *O. trifurcata* is an infrequent but naturally occurring species seen primarily in wild *Ovis* during the "spring rise." Crofton (1963) raised an interesting point when he stated that no one has discovered why this species, although it is found frequently in domestic sheep all over the world, never has been recorded in large numbers.

6. *Teladorsagia davtiani*

Teladorsagia davtiani is a common parasite of domestic sheep but has rarely been reported from wild sheep. Uhazy and Holmes (1971) reported it from 3 of 24 *O. canadensis* in Alberta and British Columbia, and Boev et al. (1963) reported it from *O. musimon* in the USSR. Becklund (1962) reported *T. davtiani* from Alaskan "sheep", presumably *O. aries*, in the Aleutian Islands. Of the 74 Dall sheep examined in this study, *T. davtiani* was encountered in only 7 animals, all in low numbers, and all from Dry Creek. *T. davtiani* has also been reported from mountain goats *Oreamnos americanus* in Alberta (Kerr and Holmes 1966) and from Alaskan caribou *Rangifer tarandus* (Becklund 1962, Neiland 1971a). Although goats do not occur in the Dry Creek area, caribou occasionally graze in the foothills of that sheep range, and it appears that *T. davtiani* was thus accidentally acquired.

7. *Nematodirus archari*

Sokolova (1948) named this species after the "arkhar" or Pamir argali *Ovis ammon polii*. *Nematodirus archari* has since been reported from *O. ammon* in Kazakhstan (Karabaev 1953) and elsewhere in the USSR (Boev et al. 1963). It has also been reported from *O. canadensis* in Alberta and British Columbia (Uhazy and Holmes 1971) and in the Wildhorse Island and Sun River areas (but not the National Bison Range) of Montana (Becklund and Senger 1967).

Becklund and Senger (1967) discussed some small differences in spicule length and in indentation of the bursal margin of their specimens of *N. archari* as compared to those Sokolova (1948) illustrated, but concluded that it was the same species. The specimens encountered in this study conformed more closely to those described by Becklund and Senger (1967): the indentation of the bursal margin between the dorsal raylets was quite clear. Becklund and Senger (1967) hypothesized that this species

> ...came with the ancestors of *Ovis canadensis* from Eurasia across the land bridge during the Pleistocene period. On this basis these nematodes may also occur in other wild sheep in Eurasia, and in *O. dalli* which ranges from Alaska southward into British Columbia.

Indeed the presence of *N. archari* in *O. dalli* was amply verified by the present study: this species was the second most numerous encountered in Dall sheep. We found an average of 109 male specimens (range 1-1180) of *N. archari* in *O. dalli*. This is in agreement with results obtained for *O. canadensis* by Uhazy and Holmes (1971) who counted an average of 156 males (range 1-1318) and Becklund and Senger who counted an average of 60 males (range 40-90). Interestingly, this species, like *M. marshalli*, was absent (supplanted?) from the National Bison Range sheep examined by Becklund and Senger (1967), although it was present in four of six bighorns from Wildhorse Island and Sun River. This species seems to be a frequent, natural parasite of wild *Ovis*.

8. *Nematodirus davtiani*

Nematodirus davtiani (also known by the suppressed name *N. rufaevastitatis* Durbin and Honess, 1951, see Becklund 1966) has been reported from *Ovis canadensis* in Alberta and British Columbia (Uhazy and Holmes 1971) and in Montana (Becklund 1966, Becklund and Senger 1967). *N. dogieli* Sokolova, 1948, a species nearly identical to *N. davtiani* except for small differences in the dorsal rays and dorsal lobes (Becklund 1966) and considered by Boev et al. (1963) to be a synonym of *N. davtiani*, has been reported in *O. ammon* and *O. ophion* in the USSR (Karabaev 1953, Boev et al. 1963). In the present study of *O. dalli*, *N. davtiani* was second in prevalence only to *M. marshalli*, although its infections generally consisted of few specimens (average = 16 males, range 1-214). Uhazy and Holmes (1971) found an average of 18 males (range 5-398) in *O. canadensis*, with a similar high prevalence. Becklund and Senger (1967) found an infection of 70 males in only 1 of 6 Wildhorse Island and Sun River bighorns, the species was absent among 12 bighorns on the National Bison Range. Becklund and Senger (1967) postulated that *N. davtiani* like *N. archari*, was a parasite of early ancestors of *Ovis* entering North America via the Bering land bridge during the Pleistocene, and hence should be present in Asian sheep and in *O. dalli*. It appears, then, that *N. davtiani* is naturally a frequent parasite of wild *Ovis*.

9. *Nematodirus oiratianus*

This species (also known by the suppressed synonym *N. lanceolatus* Ault, 1944; see Samson 1968) has been reported from *O. canadensis* in Alberta and British Columbia (Uhazy and Holmes 1971), Montana (Becklund and Senger 1967) and Colorado (Pillmore 1961, as cited by Becklund and Senger 1967); also from *O. nivicola* in Yakutia (Gubanov 1964) and *O. ammon* in Mongolia and the USSR (Boev et al. 1963). Becklund and Walker (1967b) reported it from Alaskan "sheep," presumably *O. aries*, in the Aleutian Islands. Allen (1959 and unpublished data, as cited by Samson 1968) has found in it Barbary sheep *Ammotragus lervia* introduced into New Mexico. In the present study, *N. oiratianus* was frequently encountered, averaging, however, only 19 male specimens per infection (range 1-110). Uhazy and Holmes found more abundant infections in *O. canadensis*, with an average of 47 male specimens (range 1-1490), and Becklund and Senger (1967) found an average of 582 male specimens (range 90-1690) in 6 Wildhorse Island and Sun River, Montana bighorns. Gubanov (1964) found the species in all 10 *O. nivicola* examined, with an average of 312 (male ?) specimens (range 8-1260). In comparison with these findings for *O. canadensis* and *O. nivicola*, the number of *N. oiratianus* found in *O. dalli* was relatively low. It is clear, however, that this species is a common natural parasite of wild *Ovis* in Asia and North America.

10. *Nematodirus spathiger*

Nematodirus spathiger is a common parasite of domestic sheep and cattle throughout the world. Becklund and Walker (1967b) reported the species from Alaskan sheep, presumably *O. aries*, in the Aleutians. It has also been widely reported in wild *Ovis*: *O. canadensis* in Alberta and British Columbia (Uhazy and Holmes 1971), in Montana (Becklund and Senger 1967, Forrester and Hoffman 1963), in Wyoming (Honess and Winter 1956), in Colorado (Pillmore 1961, cited by Becklund and Senger 1967), and in New Mexico (Allen and Kennedy 1952); also from *O. ammon* and *O. ophion* in the USSR (Boev et al. 1963), and from *O. musimon* in Czechoslovakia (Kotrly 1967) and the USSR (Boev et al. 1963). In *O. dalli* examined in the present study, *N. spathiger* was common: it was found in 30 of 75 Dall sheep examined, averaging 69 male specimens per infection (range 1-431). Uhazy and Holmes (1971) found the species far less frequently: 3 of 25 *O. canadensis* averaged only 29 male specimens (range 1-32). Becklund and Senger (1967), however, found numerous *N. spathiger* in 11 of 12 bighorns from the National Bison Range; the average infection was 573 male specimens (range 30-1510). They observed no *N. spathiger* among six bighorns from Wildhorse Island and Sun River, however. Becklund and Senger's (1967) findings implied that *N. spathiger* is maintained in bighorns by contact with bison or other ungulates, but our data as well as those of Uhazy and Holmes (1971) imply the species is a natural, common parasite of wild *Ovis* although not nearly as abundant as Becklund and Senger observed. It is possible the infections in sheep on the National Bison Range were unusually large because they were augmented by *N. spathiger* present in bison and other ungulates.

11. *Nematodirella* spp.

We have been able to find only a single report of *Nematodirella* spp. from wild *Ovis* sp.: Kibakin and his coworkers (1964) reported finding *N. longisimespiculata gazelli* Sokolova, 1948 in *O. ammon cycloceros* in Turkmenia. Apparently our finding of *Nematodirella* spp. in 2 of the 75 *O. dalli* examined is a first report for this species in wild *Ovis* in North America. The genus is commonly found among Alaskan moose (Neiland 1961, 1962 and 1963). Both Dall sheep infected with *Nematodirella* were from the Dry Creek area, and it is possible they harbored this nematode through exposure to infections in the moose which range in the foothills near Dry Creek.

12. *Skrjabinema* spp.

The genus *Skrjabinema* has been widely reported from wild sheep, usually as either *Skrjabinema* sp. or as *S. ovis* (Skrjabin 1915) Vereshchagin, 1926. It has been found in *O. canadensis* in western Canada (Blood 1963, Uhazy and Holmes 1971), South Dakota (Boddicker and Hugghins 1969), Colorado (Olsen and White 1949), Utah (Wilson and Honess 1965), Nevada (Allen 1964), New Mexico (Allen and Kennedy 1952, Allen 1955), and Arizona (Allen and Erling 1964). It has also been reported from *O. ammon* in Turkmenia (Kibakin et al. 1964), from *O. nivicola* in Yakutia (Gubanov 1964) and from *O. musimon* in Austria (Kutzer and Hinaidy 1969). In the present study we found 15 of 75 *O. dalli* infected with *Skrjabinema* spp., although it is felt many infections were overlooked and the actual incidence of the genus could be much higher. The average burden among 5 Dall sheep for which care was taken to count all specimens was approximately 1,700 *Skrjabinema* of both sexes (range 435-4561). In *O. canadensis*, Allen and Kennedy (1952) found "approximately 3,000" specimens in one sheep; in 1955 Allen found a range of 10 to 1,026 *Skrjabinema* in 8 of 9 bighorns; and Uhazy and Holmes (1971) found a single specimen in each of 2 bighorns, of 25 total examined. Gubanov (1964) found an average of 289 *Skrjabinema* (range 1-1015) in all 10 *O. nivicola* he examined. Apparently this genus is a common and abundant, but frequently overlooked, natural parasite of wild *Ovis*.

13. *Trichuris* spp.

Trichuris has frequently been reported from wild *Ovis*, often identified as a variety of species: *T. capreoli* (Artiukh 1948), *T. discolor* (von Linstow 1906) Ransom, 1911, *T. globulosa* (von Linstow 1901) Ransom, 1911, *T. ovis* (Abildgaard 1795) Smith, 1908, *T. schumakovitschi* (Savinkova 1967) and *T. skrjabini* Baskakov, 1924. Most Russian authors prefer the generic name *Trichocephalus* Schrank, 1788, which is morphologically more accurate, but *Trichuris* has priority under the rules of nomenclature (Levine 1968). The genus has been reported from *O. canadensis* in Alberta and British Columbia (Blood 1963, Uhazy and Holmes 1971, Knight and Uhazy 1973), Montana (Couey 1950), Wyoming (Honess and Winter 1956), Idaho (Quortrup and Sudheimer 1944), South Dakota (Boddicker and Hugghins 1969), Nevada (Allen 1964) and New Mexico (Allen and Kennedy 1952, Allen

1955). It has also been reported in *O. ammon* in Turkmenia (Kibakin et al. 1964), in *O. musimon* in Germany (Boch and Horchner 1962), Austria (Kutzer and Hinaidy 1969), Czechoslovakia (Kotrly 1967) and the Crimea (Roukhladev, in Ianouchko 1955), in *O. ophion* in Azerbaidzhan (Gusienov and Asadova 1966), and in *O. nivicola* in Yakutia (Gubanov 1964). In the present study of *O. dalli*, 14 of 18 carefully examined sheep harbored *Trichuris* sp. averaging 13 per infection (range 2-44). This is very similar to Gubanov's (1964) finding of an average of 16 *Trichuris* (range 2-33) for *O. nivicola*. Uhazy and Holmes (1971) found this nematode in abundance in *O. canadensis*: an average of 20 specimens but a range of 1-371. Allen and Kennedy (1952) reported 5 *Trichuris* in a single *O. canadensis*, and Allen (1955) reported a range of 1-12 *Trichuris* in 6 bighorns. It appears that *Trichuris* is a common parasite of wild *Ovis* although in most cases it is not abundant.

The following species found in *O. dalli* in the present study appear to be natural parasites of wild *Ovis: Marshallagia marshalli, Ostertagia circumcincta, O. occidentalis, O. trifurcata, Nematodirus archari, N. davtiani, N. oiratianus, N. spathiger, Skrjabinema* spp. and *Trichuris* spp. Bison probably can be held responsible for the rare occurrence of *Ostertagia ostertagi* in *O. dalli*, caribou may similarly be responsible for the occasional appearance of *Teladorsagia davtiani*, and moose for the appearance of *Nematodirella* spp. in Dall sheep.

B. Wild *Ovis* as Reservoirs and Accidental Hosts

Because Dall sheep have had almost no contact with imported domestic livestock, an examination of their parasitic fauna provides valuable information. Not only does the fauna of *O. dalli* indicate which nematode species may occur naturally and independently in wild sheep, but also the fact that certain nematode species which might be expected in *O. dalli* were not found provides clues as to the transmission and ecological requirements of these absent species. A total of 31 species belonging to 12 genera have been reported from *Ovis canadensis, O. nivicola, O. ammon, O. ophion, O. vignei* and *O. musimon*, but were not encountered in the present study of *O. dalli* (see Appendix).

Becklund and Senger (1967) found two species of *Cooperia* Ransom, 1907, i.e. *C. oncophora* (Railliet 1898), Ransom 1907 and *C. surnabada*, in *O. canadensis* from the National Bison Range. This is virtually the only report of this genus in wild sheep, although *C. pectinata* Ransom, 1907 has been reported from *O. musimon* in Austria (Kutzer and Hinaidy 1969). *Cooperia* is common in domestic sheep and in American antelope *Antilocapra americana* (Honess and Winter 1956). This species probably occurs only accidentally in wild *Ovis*, and in large numbers only when conditions are favorable for multiple reinfection from other species, as on the National Bison Range. Crofton (1963) considers the genus to be present only in warm climates.

Haemonchus contortus (Rudolphi 1803) Cobb, 1898 and *H. placei* (Place 1893) Ransom, 1911 are even more serious problems in domestic sheep in warm climates. Jehan and Gupta (1974) found 10°C to be the lower limit for development of larval *H. contortus*, which would inhibit the occurrence of the species in Alaska. *H. contortus* has been reported from *O. canadensis* in Wyoming (Honess and Winter 1956), *O. ammon* in the USSR (Boev et al. 1963), and *O. musimon* in Germany (Boch and Horchner 1962), Austria (Kutzer and Hinaidy 1969) and Czechoslovakia (Kotrly 1967). *H. placei* has been reported from *O. canadensis* in New Mexico (Allen 1955). All of these infections could be ascribed to contact between wild *Ovis* and domestic livestock. Heavy infections have not been encountered in game animals unless the host species was densely concentrated (Honess and Winter 1956).

Various species of *Ostertagia* have been reported for wild *Ovis* which were not encountered in *O. dalli*. *Ostertagia lyrata* Sjoberg, 1926 has been reported from *Ovis canadensis* only by Becklund and Senger (1967) on the National Bison Range, and Boev and coworkers (1963) reported the species in *O. musimon* in the USSR. *O. lyrata* is primarily a parasite of cattle and probably occurs only secondarily in wild *Ovis*. *Ovis musimon* has been reported to harbor a number of species of *Ostertagia*: *O. crimensis* Kadenatsii and Andreeva, 1958 (Levine 1968), *O. davtiani* Grigorian, 1951 (Boev et al. 1963), *O. gruehneri* Skrjabin , 1929 (Roukhladev, in Ianouchko 1955), *O. leptospicularis* Assadov, 1953 (Kotrly 1967) and the related species *Mouflonagia podjapolskyi* Schulz, Andreeva and Kadenatsii, 1954 (Schulz, Andreeva and Kadenatsii 1954 as cited in Levine 1968, Boch and Horchner 1962) which have not been encountered in other wild *Ovis*. *Ostertagia orloffi* Sankin, 1930 has been reported from *Ovis ammon* in the USSR (Boev et al. 1963, Karamendin 1967), and has been seen in mule deer *Odocoileus hemionus*, domestic sheep and cattle in Colorado and Wyoming but not in wild *Ovis* species (Honess and Winter 1956).

Pseudostertagia bullosa Orloff, 1933, a parasite of antelope in the western United States, is secondarily transmitted to domestic sheep in that area (Lucker and Dikmans 1945). It is not common in domestic sheep (Olsen 1950) and has been reported only twice from *O. canadensis* in Colorado (Pillmore 1961) and New Mexico (Allen 1955).

Skrjabinagia (Kassimov 1942) Altaev, 1952, a genus very similar to *Ostertagia*, has been reported only once from wild *Ovis*: Kutzer and Hinaidy (1969) recorded it from *O. musimon* in Austria. *Spiculopteragia bohmi* Gebauer, 1931 and *S. spiculoptera* (Guschanskaya 1931) Orloff, 1933, parasites of domestic and wild ruminants in Europe, have been reported in *O. musimon* in Germany (Boch and Horchner 1962) and in the Crimea (Roukhladev, in Ianouchko 1955).

Trichostrongylus Looss, 1905 has been widely reported from wild *Ovis*. Becklund and Senger (1967) found some female *Trichostrongylus* sp. (?) in *O. canadensis* on the National Bison Range: this is the only report from *O. canadensis* outside of zoos. In the USSR, *O. ammon* has been reported to harbor *T. columbiformis* (Giles 1892) Ransom, 1911 and *T. probolurus* (Railliet 1896) Looss, 1905, while *O. ophion* harbors *T. columbiformis*, *T. skrjabini* Kalantraian, 1930 and *T. vitrinus* Loss, 1905 (Boev et al. 1963). *Trichostrongylus axei* (Cobbold 1879), *T. capricola* Ransom, 1907, *T. columbiformis* (Giles 1892) Ransom, 1911 and *T. vitrinus* have been reported for *O. musimon* (see Appendix). The free-living larval stages of this genus are not adapted to surviving cold, arid conditions, which may explain its absence in wild *Ovis* in the cool-temperate and subarctic zones (Kates 1950).

The absence of *Nematodirus abnormalis* May, 1920 in this study of *Ovis dalli* was rather surprising. Becklund and Walker (1967a, 1967b) reported this species from Alaskan "sheep," presumably *Ovis aries* in the Aleutians. Honess and Winter (1956) reported *N. abnormalis* in *O. canadensis* in Wyoming, but both Uhazy and Holmes (1971) and Becklund and Senger (1967) failed to find this species in their examinations of *O. canadensis* in Alberta, British Columbia and Montana. Boev, Lavrov and coworkers (1957), as cited by Gvozdev (1968) and Boev et al. (1963) reported *N. abnormalis* in *O. ammon, O. ophion* and *O. vignei* in the USSR, all in areas where domestic sheep are common. It is possible this species is primarily a parasite of domestic sheep and occurs only secondarily in wild *Ovis*.

Nematodirus filicollis Rudolphi, 1802 has rarely been found in wild sheep outside of Europe. Cowan (1951) gave the only report of this species from *O. canadensis*. Kibakin and coworkers (1964) reported it from *O. ammon* in Turkmenia, and it has been reported in *O. musimon* in Germany (Boch and Horchner 1962), Austria (Kutzer and Hinaidy 1969) and Czechoslovakia (Kotrly 1967).

Nematodirus helvetianus, like *Ostertagia ostertagi*, is primarily a parasite of cattle and bison, although Kibakin and his coworkers (1964) found it in *Ovis ammon* in Turkmenia and Becklund and Senger (1967) found it in 4 of 12 *O. canadensis* on the National Bison Range. In both of these cases it appears that the species was introduced to wild sheep from domestic cattle (Turkmenia) or bison (Montana), since *N. helvetianus* has not been observed in sheep without these contacts (Becklund and Senger 1967, Uhazy and Holmes 1971). There is some evidence indicating sheep are resistant to *N. helvetianus* as they are to *Ostertagia ostertagi* (Herlich and Stewart 1954).

Becklund (1965) described a new trichostrongylid from the mountain goat which he named *Nematodirus maculosus*. Uhazy and Holmes (1971) encountered this parasite in one of the 25 *O. canadensis* they examined in Alberta. This is the only report of this species from wild *Ovis*; apparently *N. maculosus* occurs primarily in the mountain goat (Kerr and Holmes 1966). Although the ranges of the Dall sheep examined in this study from the Kenai Peninsula occasionally overlap with the range of mountain goats, this parasite was not encountered.

Becklund and Senger (1967) reported a new species of *Nematodirus* from *O. canadensis* on the National Bison Range which they named *N. odocolei* (Becklund and Walker 1967a). Becklund and Walker (1967a) considered this species to be a normal parasite of mule deer in western central North America, occurring only secondarily in wild *Ovis*.

Nodular worms of livestock belonging to the genera *Chabertia* Railliet and Henry , 1909 and *Oesophagostomum* Molin, 1861 have only rarely been encountered in wild *Ovis*: Allen (1955) tentatively identified a single *Oesophagostomum* sp. larva in *O. canadensis* in New Mexico, and both genera have also been reported for *O. ammon* in Turkmenia (Kibakin et al. 1964) and *O. musimon* in Germany (Boch and Horchner 1962), Austria (Kutzer and Hinaidy 1969) and Czechoslovakia (Kotrly 1967). There is a single report of the hookworm *Bunostomum trigocephalum* (Rudolphi 1808)

Railliet, 1902 in *O. musimon* in Germany (Boch and Horchner 1969), and of the threadworm, *Strongyloides papillosus* (Wedl 1856) Ransom, 1911, also in *O. musimon*, in Austria (Kutzer and Hinaidy 1969).

In general the species present in wild *Ovis* which were not encountered in *O. dalli* were either not adapted to larval survival in cold, arid subarctic environments with short summers, or were absent because they are primarily parasitic in domestic livestock and apparently occur only secondarily in wild *Ovis*.

Many of the studies of wild *Ovis* have been undertaken to ascertain the parasite species for which wild sheep were "reservoir hosts." However, because these studies were made in areas where contact between wild sheep and domestic livestock was already long established, it was usually impossible to determine whether wild sheep originally introduced certain parasites into the domestic animals or vice versa. Karabaev (1953) found that domestic sheep introduced to the Bet-Pak-Dala Plateau of central Kazakhstan were rapidly freed of certain parasites (*Haemonchus*, *Bunostomum*, etc.) but acquired new species (*Nematodirus archari*, *N. dogieli*, etc.) from wild ungulates of the area, among them *O. ammon*. Becklund and Senger (1967) found totally different parasite faunas in *O. canadensis* from the National Bison Range, Wildhorse Island and Sun River. They suspected the different faunas were due to different herd origins, but Uhazy and Holmes (1971) studied *O. canadensis* in Banff National Park, the origin of the National Bison Range sheep herd, and found a parasite fauna the same as that of the Wildhorse Island and Sun River sheep. Uhazy and Holmes felt it was probable that the wild sheep transplanted into the National Bison Range had acquired new parasites from ungulates already established there. Becklund and Senger's (1967) data then imply that all of the original "natural" parasite species (*Marshallagia marshalli*, *Ostertagia circumcincta*, *O. occidentalis*, *Nematodirus archari*, *N. davtiani* and *N. oiratianus*) were supplanted by the new species. Exactly how this supplanting occurred, whether by the effects of larval microhabitat, climate, crowding, etc., has yet to be explained.

C. Physical Separation of the Nematode Species

Although a total of 14 nematode species were encountered in the gastrointestinal tract of *O. dalli*, these species were in many cases physically separated within the tract. Six species, *Marshallagia marshalli*, *Ostertagia circumcincta*, *O. occidentalis*, *O. ostertagi*, *O. trifurcata* and *Teladorsagia davtiani*, were all found in the abomasum with only small numbers washed down (possibly postmortem) into the duodenum and anterior small intestine. On a single occasion, 50% of the *M. marshalli* encountered in a ewe taken in May were found in the lower digestive tract. This was felt to be an example of purging associated with the "spring rise" phenomenon . When records were kept separately for the fundic and pyloric portions of the abomasa of two sheep, adult trichostrongylids were encountered abundantly in both areas, but immature forms were overwhelmingly found in the pyloric portion. This is consistent with the findings of Sommerville (1953). Dunsmore (1966) found that developing larvae invade the fundic area only during heavy secondary infections when a possible local reaction prevents their establishment in the pylorus. There appears to be little physical separation between the six species inhabiting the abomasum, but they tend to be temporally separated by seasonal effects, as discussed subsequently.

One of the most interesting findings of this study was the apparent physical separation within the small intestine of the four species of *Nematodirus* found in *O. dalli*. Nearly all of the prevalent but non-numerous *N. davtiani* were found in the pyloric abomasum, duodenum and first meter of the small intestine. The common and abundant *N. archari* was almost exclusively (96%) restricted to the duodenum and first three meters of the small intestine. *N. oiratianus* was found distributed along the first four meters of the small intestine, with slightly more in the third and fourth meters. Finally, *N. spathiger* was found primarily (93%) in the posterior three-fourths of the small intestine. Thus there is essentially no overlap between the most anterior species, *N. davtiani*, and the posterior species *N. spathiger*. *Nematodirus oiratianus* and *N. archari* tend to overlap each other and, to some extent, *N. davtiani*. Only *N. oriatianus* inhabits the digestive tract near "the habitat" of *N. spathiger*. These specific habitat preferences may be related to differences in larval development within the mucosa and to the large variations in chemical environment and acidity along this section of the gut. Clearly the subject should be further investigated.

The final three genera, *Nematodirella*, *Skrjabinema* and *Trichuris*, inhabit the caecum and upper colon. *Nematodirella* occurred rarely and normally is a parasite of the small intestine, so its presence in the caecum and colon may indicate it was an accidental parasite being passed out of the body. *Skrjabinema* spp. are similar to other pinworms common in many animals and occurring also in humans. Adult pinworms feed on the contents of the caecum and upper colon, usually causing no harm to the host even if present in large numbers. But immature *Skrjabinema* develop in the caecal mucosa, where large numbers of larvae could be pathogenic. Very little is known about this genus. *Trichuris* is much better known, and Burrows and Lillis (1964) have demonstrated that the species *T. vulpis* (Froelich 1789), at least, is an avid bloodsucker. Adult *Trichuris* weave their slender anterior ends into the caecal mucosa, and probably rarely encounter *Skrjabinema* which are out in the lumen of the organ. However, the larval stages may overlap because the larvae of *Trichuris* also develop within the caecal mucosa (Beer 1971). The nodules encountered in several of the Dall sheep examined, which could represent inflammatory reactions around larval development sites, have already been described.

D. Temporal Separation of the Nematode Species

1. The Spring Rise and Larval Inhibition

The data from sheep from the Kenai Peninsula in 1970-71 indicated that both *Nematodirus* spp. and *Ostertagia* spp. were more abundant in late winter (February and March) than in November. The material from Dry Creek demonstrated a large increase in *Nematodirus*, particularly *N. archari* and *N. spathiger*, in April and May. In June and July, *Ostertagia* spp. became more abundant. These findings are consistent with the well-known "spring rise" phenomenon seen in domestic sheep, when fecal nematode egg counts increase markedly around lambing time. When ewes lamb in the fall, similar rises occur at that time, indicating that the increase is "peri-parturient" (Crofton 1958, Southcott et al. 1972, Vlasoff 1973). It is now believed that the increase is influenced by an interaction between the reproductive cycle and the immune status of the individual animal (Crofton 1963, Cvetkovic 1971). The data from Dry Creek tend to support this view because pregnant ewes averaged nearly twice the trichostrongylid burden of nonpregnant ewes, although there was considerable individual variation. However, some investigators have found a noticeable "spring rise" occurring in nonpregnant ewes and rams (Gibbs 1968, Levine 1968). In the present study we also found heavier infections in nonpregnant ewes during the spring than in the winter.

The "spring rise" in Dall sheep is probably due to a complex of factors. Nutritional stress, associated with environmental conditions in the late winter and early spring, lowers the resistance of all animals, especially of pregnant ewes carrying near-term fetuses. Lowered resistance invites an increase in the trichostrongylid fauna, although there is some evidence that a specific host stimulus may be responsible (Blitz and Gibbs 1971). When the first *Nematodirus* and *Ostertagia* appear in the digestive tracts in February and March, however, conditions on the sheep range in Alaska are still too cold for larval development. It is probable that, instead, these increases in the adult nematode fauna are due to the maturation of "inhibited larvae," or larvae which have infected the sheep during the previous spring and summer but have remained within the mucosa in a state of arrested development. Brunsdon (1972) has demonstrated how the proportion of inhibited larvae of *Ostertagia* within the mucosa gradually increases during the autumn and winter, reaching a peak in the spring. The phenomenon of larval inhibition has been extensively studied in *Ovis aries* (see Levine 1968, also Crofton 1963, Wright et al. 1973). Michel and coworkers (1973a) showed that the offspring of nematodes which had been inhibited larvae had a greater propensity themselves for inhibition, and in another study the same authors (1973b) found evidence that a host's previous experience of infection tended to increase the proportion of larvae which were inhibited. Vural et al. (1972) determined that fully one-third of the infective larval *Marshallagia marshalli* given to young sheep were inhibited in the early fourth stage of development one month after infection.

Besides the maturation of inhibited larvae, lower host resistance in late winter also leads to an increase in egg output by the adult worms already present in the sheep (Cushnie and White 1948, Naerland 1952, Michel 1967, Levine 1968). Thus more infective larvae are present on the pasture, and both *Marshallagia* and *Nematodirus* eggs and larvae are uniquely adapted to survival under the cold, arid conditions characteristic of Dall sheep range during the early spring. Both genera have large eggs, and the morula is in an advanced stage when passed out of the female (Dunn 1969). In both genera the first two larval moults occur within this egg, with very little larval growth (Levine 1968), and the larvae are protected within the shell from dessication and temperature extremes. Sarwar (1952) has reported the survival of *Marshallagia marshalli* near Tibet at 18,000 feet under conditions of extreme cold and aridity. It has even been shown that some *Nematodirus* eggs can hatch only after a period of freezing followed by warmer temperatures (Crofton 1963). Finally, both genera have very long prepatent periods (approximately three months, although frequently the larvae can pass the entire winter within the shell before hatching). This long prepatent period tends to reduce the number of generations that can infect sheep in temperate climates and other more rapidly developing genera tend to be more common there, but the adaptation is ideal for the long winters and short summers characteristic of subarctic sheep ranges. Thus Dall sheep in early spring are liable to ingest more trichostrongylid eggs not only because the egg output of adult worms in their digestive tract increases, but also because *Marshallagia* and *Nematodirus* eggs which have survived the winter are made available as the snow melts. Since *Marshallagia* numbers remain fairly constant throughout the year, this mechanism is probably more important for species of *Nematodirus*.

Species of *Ostertagia* develop in the typical trichostrongylid manner, hatching from the egg in a day or less depending on the temperature (Crofton 1965). They undergo two moults before ensheathing into the third (infective) stage. Eggs do not hatch below 5°C, and larvae are not very resistant to dessication (Crofton 1963). Thus it is reasonable that species of *Ostertagia* do not increase substantially in Dall sheep until June and July, when conditions are favorable for their larval development on the pasture.

Thus the trichostrongylid species infecting *Ovis dalli* are somewhat separated in time. Species of *Ostertagia* are common only in the late spring and summer, they pass the winter as inhibited larvae to appear in the spring when host resistance is low. Species of *Nematodirus* appear slightly before *Ostertagia* in the spring because of their greater resistance to cold and dessication; the development of inhibited larvae may also play an important role. *Nematodirus* may tend to be uncommon by late autumn because, due to the long time required for development, it manages only a single generation per year (Crofton 1963). This sequence of increase in *Nematodirus* during the spring followed by a later increase in *Ostertagia*, with low levels of both genera in the winter, has also been observed in New Zealand domestic lambs (Brunsdon 1970).

Marshallagia appears to be able to maintain a nearly constant level of infection year-round. The mechanism by which this is accomplished has not been investigated, but a carefully regulated system of larval inhibition is probably involved. The long prepatent period and larval resistance to cold and dessication characteristic of this genus are also important factors.

The data on sheep from Dry Creek indicate that *Skrjabinema* was more common and abundant in late spring than in November. Although very little is known about larval tolerances in this genus, the large number of pinworms encountered in April 1973 before pasture conditions were favorable for larval development was of particular interest. It is possible that larvae of *Skrjabinema*, like *Ostertagia*, remain in the gut mucosa in a state of inhibited development until host resistance drops in the late winter. Specimens of *Trichuris* spp. were also more frequent in the spring; this was also the time when nodules were encountered in the mucosa. Eggs of *Trichuris vulpis* do not survive extremely cold temperatures well, but little is known about the ova of other species of *Trichuris*. Opitz (1963) postulated that two larval stages develop within the egg of *T. ovis* before it hatches; this would tend to enhance its overwinter survival.

2. Seasonal Migrations of the Host

An important difference between wild and domestic *Ovis* is that the latter are usually artifically confined in far greater concentrations than would ever be encountered in wild sheep. Domestic sheep are moved from pasture to pasture by herders, and the disease-producing effects of crowding are held in check by medication. In contrast, bighorn sheep quickly succumb to disease, often the lungworm-pneumonia complex, when their range becomes overcrowded. Certainly the trichostrongylid load increases dramatically in wild sheep with restricted ranges simply because the animals repeatedly reinfect themselves on vegetation contaminated with nematode eggs. Osipov et al. (1973) have described such a situation in domestic sheep in the USSR when farming practices reduced available pasture area. Overcrowding will, of course, also reduce range quality which, aside from the obvious nutritional effects, will have an additional insidious effect. When forage is poor in quality, sheep will crop it more closely to the ground, thus ingesting large numbers of infective larvae even in microclimates which do not allow the larvae to migrate more than a few millimeters up the grass blades (Dunn 1969). Because of urbanization and development in the western U.S., overcrowding on reduced pasture area is one of the most serious problems facing *Ovis canadensis*. Fortunately, most Alaskan *O. dalli* ranges are not yet overcrowded.

The seasonal migrations of Dall sheep over their home ranges determine how long and how often the sheep revisit any one pasture where feces have been deposited and infective larvae are present on the vegetation. If a sheep herd ranges widely, such a long time may pass between visits to a certain pasture that no viable infective larvae remain. Alaskan Dall sheep, however, occur in small distinct subpopulations which usually restrict their annual movements to particular traditional pastures, mineral licks and bedding areas. Since the animals tend to defecate while eating or when arising from sleep (Honess and Frost 1942), these habits perpetuate gastrointestinal helminth infections within the subpopulations.

Annual movements of the Kenai Peninsula sheep have been described to some extent by Nichols (Nichols and Smith 1971, Nichols and Heimer 1972). Nichols (Nichols and Heimer 1972) working with R. Hansen (of Colorado State University), determined that sites used as summer range by the Kenai Peninsula Dall sheep are those covered with snow drifts during the winter, while winter range is generally wind-scoured ridges. But in general the three herds studied on the Kenai Peninsula tend to be separate and restricted to relatively small areas: Cooper Landing closed area, Surprise Mountain and Crescent Mountain (Nichols and Smith 1971).

Heimer (1973) has discussed in detail the seasonal movements of Dall sheep in the Dry Creek area. He found there were several distinct subpopulations of ewes and of rams. These small subpopulations graze on the winter range between November and early May. Between early May and early July, depending on snow conditions, is a transition period during which these sheep utilize mineral licks and move into summer range, where they graze between July and October. Some of the small subpopulations overlap on the summer ranges, and considerable contact between subpopulations can occur at the mineral licks. In most cases the summer and winter ranges are separate, but some subpopulations utilize winter range throughout the year, with summer range simply added to the area available in winter. Bands of ewes and lambs remain separate from ram bands during the summer but mingle during the rut and remain together through the winter.

The traditional annual range use pattern of sheep favors trichostrongylids like *Marshallagia* and *Nematodirus*, seen so abundantly in this study, which can overwinter and survive where they are deposited until the sheep graze on the same pasture during the next year. Species of *Ostertagia* have eggs and larvae less well adapted to survival on pasture, and larval inhibition provides an important source of "new" *Ostertagia* infections in the spring until conditions again become favorable for larval survival and development on the pasture. The eggs and larvae of *Trichuris* spp. are somewhat resistant to cold (Opitz 1963), but little is known about their survival on pasture. Larval inhibition, as possibly represented by the caecal nodules, could be important in the overwintering of this genus also. Nothing is known about the survival of eggs and larvae of *Skrjabinema*.

Gastrointestinal nematodes do not become abundant in Dall sheep populations as a whole because their traditional use areas are still large enough that infective larvae are not concentrated. Mineral licks, however, represent a possible exception. Heimer (1973) found that ewes with lambs use the licks most frequently, and do so during the very period of the "spring rise" phenomenon. The small area of the lick, utilized by many sheep, may quickly become filled with infective nematode larvae. Licks may serve to spread nematode species among various subpopulations that otherwise have little contact.

E. Pathogenicity of the Gastrointestinal Nematodes

1. Physical and Physiological Effects on the Host

Specific pathogenic characteristics of the various trichostrongylid, pinworm and whipworm species have already been discussed, but the general effects of these infections on the host will now be considered. Of primary importance is that severely pathogenic nematodes simply do not occur independently among wild sheep because of the strong pressures of natural selection. If such infections are found in wild sheep it usually can be assumed that they were acquired from a domestic livestock source. The usual pathogenic situation is rather one of chronically weakening the sheep, with considerable individual variation among sheep in the severity of effect. Selection acts on both host and parasite to keep gastrointestinal helminth infections in the population as a whole at a low and stable level. Any unusual environmental factor influencing either the general condition of the host or larval survival on pasture, such as heavy snow or rain, long periods of extreme cold or vegetational changes, can radically alter this balanced host-parasite situation.

The physical and physiological effects of trichostrongylid infections, particularly abomasal infections, have been intensively studied in domestic sheep because wool and meat production are affected. Physical signs of moderate gastrointestinal nematode infections include thirst, watery discharge around the eyes, loss of appetite, abdominal pains, weight loss (or failure to gain weight in lambs) and diarrhea (Kates and Turner 1953, Osipov 1962, Armour et al. 1966, Levine 1968, Dunn 1969, Anderson 1972, Ciordia et al. 1972, Anderson 1973). There is a considerable effect on wool production among infected sheep. The wool fiber decreases in diameter and loses its resiliency (Levine 1968, Bergstrom and Kinnison 1971, Anderson 1972, Fudalewicz-Niemczyk et al. 1972, Rowlands and Probert 1972, Anderson 1973, Barger et al. 1973). These symptoms increase in severity as the level of infection increases.

Damage to the mucosa of the abomasum and small intestine is the prime effect of trichostrongylid infections. The mucosa appears hemorrhagic, thickened and edemic, with raised nodules and tiny red pits on the inner surface and thickened, deepened fundic folds (Osipov 1962, Armour et al. 1966, Levine 1968, Buzmakova and Sosipatrov 1971, Mulligan 1972, Anderson 1973, Coop and Mapes 1973, Coop et al. 1973, McLeay et al. 1973). Blood sucking adults damage the mucosa slightly as they feed, but most of the damage is caused by the disruptive actions of developing larvae which burrow into the gastric pits. As larvae grow they stretch the pits, causing epithelial hyperplasia, cell damage and necrosis. Lymphocytes and eosinophils infiltrate the area. Damaged cells become necrotic and are sloughed off, to be replaced by undifferentiated, nonfunctional cells. The canaliculi through which the parietal cells secrete HCl and KCl are disrupted and do not empty into the lumen (McLeay et al. 1973). Larvae and young adults leaving the mucosa produce wounds and pits, and larvae mistakenly penetrating the lamina propria instead of the lumen induce granulomatous foreign body reactions which appear as dark spots at necropsy (Armour et al. 1966, Buzmakova and Sosipatrov 1971). These pathological signs were frequently observed to a mild extent in the pylorus and duodenum of Dall sheep in this study.

All of these physical changes, of course, produce physiological changes. Because of the loss or inhibition of the parietal cells, which are affected both by larval damage and by inhibitory secretions from adult nematodes (McLeay et al. 1973), the abomasal pH increases (Armour et al. 1966, McLeay et al. 1973). There is a reduction in the activity of important abomasal and duodenal enzymes: dissacharidase, maltase, alkaline phosphatase and leucine amino peptidase (Coop and Mapes 1973, Coop et al. 1973, Mapes and Coop 1973). These changes lead to decreased absorption of calcium and protein, with a consequent loss of nitrogen (Mulligan 1972, Barger 1973, Parkins et al. 1973). An increase in the sodium concentration of the abomasal contents has also been observed (Armour et al. 1966, McLeay et al. 1973).

These physical and physiological effects are reflected in the blood. The concentrations of protein, albumin and inorganic phosphate in the serum decrease, while the plasma urea and gamma globulin levels increase. Plasma pepsinogen leaks out of the damaged mucosa and appears in the plasma (Armour et al. 1966, Anderson 1972, Anderson 1973, McLeay 1973).

The general impact of these physiological changes is to reduce the digestibility of crude proteins and dry matter (Levine 1968, Dunn 1969). When this is coupled with the general decline in appetite associated with moderate infections (Levine 1968, Dunn 1969, Rowlands and Probert 1972, McLeay et al. 1973), trichostrongylids can have serious effects on the nutrition of wild sheep. During the summer months, when nutritious forage is available, the sheep may be able to compensate for these effects (Dunn 1969). But in late winter and early spring when *Nematodirus* and *Ostertagia* begin to appear, reduction in digestive capabilities and appetite will have serious consequences for animals already on a low-quality diet and in poor condition otherwise.

Thus, although the most seriously pathogenic nematodes known in domestic sheep are not encountered in wild sheep, those species reported for *O. dalli* and other wild sheep can have serious effects. Small or moderate numbers of parasites acting in conjunction with social, nutritional and disease factors can chronically depress the hosts' condition to the point that it succumbs to accident, predators or winter stresses where it otherwise might have survived. Wild sheep harboring parasite levels approaching those considered pathogenic for domestic sheep will probably not survive to be collected for examination.

2. Host Age, Immunity and Resistance

There is considerable variation among wild sheep in the severity of chronic infections of gastrointestinal nematodes. This is due to variations in host resistance. Genetically based resistance transmitted by the sire has been examined by Whitlock (1955), and there is evidence that different breeds of domestic sheep vary considerably in their resistance to single nematode species (Dunn 1969). Immunologically acquired resistance, however, is the prime subject of current interest. The process of developing immunity to helminth infections in the gastrointestinal tract is considerably more complicated and less efficient than developing immunity to bacterial infections. First, the body does not respond as strongly to foreign proteins (nematodes) in the digestive tract, for obvious reasons, as it does to proteins (bacteria) in the tissues. Second, gastrointestinal nematodes always have free-living stages and are therefore less vulnerable than bacteria, which grow and reproduce entirely within the host. Finally, there is the complex nature of the antigenic stimulus associated with nematodes. A nematode is a very large body of structural, physiological and secreted materials relative to a bacterium. It is against the secreted materials that the host can best produce antibodies. Although secretions from the esophagus, anus, reproductive tract and excretory pore can all act as antigens, it is larval exsheathing fluid against which the host can apparently respond most vigorously and effectively (Levine 1968). Thus immunological defenses concentrate on the developing larvae, which are, in any case, more destructive than the adults.

Upon ingesting infective larvae, a resistant host may completely reject the infection, may allow an initial invasion of the gastrointestinal mucosa but then inhibit the development of the larvae, or may at least prolong the prepatent period (Dunn 1969). For these reasons resistant sheep generally harbor fewer nematodes, all of which are smaller in size and less fecund than those harbored in less resistant hosts (Dunn 1969). Michel (1963) has carefully demonstrated and discussed how resistant hosts (calves) inhibit the development, growth and ovulation of *Ostertagia ostertagi*. He found that adult *O. ostertagi* were stunted, that female nematodes contained fewer eggs than normal, and that fewer females developed to the adult stage than males, which had a marked effect on total fecundity. Another of the most obvious manifestations of host resistance is the "self cure" phenomenon, when the large numbers of gastrointestinal nematodes building up during the "spring rise" are spontaneously eliminated (Crofton 1963, Soulsby 1965, Levine 1968, Dunn 1969).

How is resistance to gastrointestinal helminth infection acquired and why does it differ in degree from host to host? It is widely recognized that although a small amount of antibodies to strongylate infection are transferred to newborn lambs in the colostrum (Dunn 1969), resistance to infection is primarily a function of previous infection experience. Kelley (1973) has discussed, physiologically, how immunogenic parasite antigens cause the formation of circulating immunoglobulin and sensitized lymphocytes. This has been substantiated by finding that a single large dose of infective larvae results in a larger parasite burden than if the same number of larvae are administered in small doses over a period of time so immunity can build up (Michel 1963, Donald et al. 1964, Dineen et al. 1965, Goldberg 1973a, b and c, Michel et al. 1973a). Once an animal has experienced a primary infection, it is sensitized in the typical immunological manner so that the antigenic threshold of immune response to later infections is considerably reduced (Donald et al. 1964, Dineen et al. 1965). However, Donald et al. (1964) have determined that the relationship between host and parasite has probably evolved to the point that below a certain level of infection (the "threshold of response") the host will not immunologically respond against the parasite. This tolerance of a low level of infection permits the parasite species to survive and reproduce while at the same time it limits the size of the total burden and thus minimizes pathogenic effects.

There are indications that each individual species of nematode requires a separate immunological response system, because species vary in both the developmental point at which larvae are inhibited and also in the intensity and degree of antigenic stimulation required to produce an immune response (Michel 1963). Michel (1963) believes these differences constitute a possible explanation for many of the large epidemiological differences encountered among the trichostrongylid species. Although the self-cure phenomenon, where large numbers of only one species may trigger the expulsion of several species, does not seem to be species-specific, the phenomenon may be explained by cross reactivity among shared or chemically related antigens in each of the purged species

(Soulsby 1965). If a host is heavily infected with other trichostrongylids, the level at which it immunologically responds to one particular species may be affected.

Resistance to gastrointestinal nematodes is a dynamic state. Even a drastic decline in nutrition does not affect the resistance of immune animals (Dunn 1969). This point was substantiated in this study when no indications were seen that Dall sheep which were smaller in weight (excluding lambs) or had low marrow fat content, harbored, in general, more gastrointestinal nematodes. There is some evidence, however, that immunity is gradually lost in the absence of antigenic stimulus (Michel 1963). Such a loss would explain the "spring rise" phenomenon seen in pregnant ewes with previous infection experience, because infections are often minimal or absent during the early and mid-winter months (Dunn 1969, Brunsdon 1971, Cvetkovic et al. 1971, Barger et al. 1973).

One of the most important considerations to be drawn from this brief discussion of resistance and immunity is that young animals with no previous infection experience are the most vulnerable. Although newborn lambs may receive a small dose of antibodies in the colostrum, they are apparently unable to begin developing their own resistance to infection until approximately three months of age (Seghetti and Senger 1958, Soulsby 1965, Dunn 1969, Gibson and Parfitt 1972). During this dangerous period the lamb is continuously in close contact with its mother, and it has been demonstrated the ewe is an important source of lamb infection (Lewis et al. 1972, Donald and Waller 1973). Lewis et al. (1972) found that the earlier lambs were weaned (beginning at three weeks of age), the smaller their trichostrongylid burden. Resistance to infection begins to develop at three months of age, and by the age of nine months it is highly developed (Armour et al. 1966, Dunn 1969, Gibson and Parfitt 1972).

Unfortunately the "spring rise" phenomenon and the increase in *Ostertagia* and *Nematodirus* in ewes correspond precisely with the lambs' period of greatest susceptibility to infection. All lambs probably become infected, particularly those whose mothers are heavily infected. If the infection becomes serious, it can, in conjunction with other stresses, ultimately be fatal for weak lambs. In most cases, however, the lamb probably ingests a moderate amount of infective larvae, but in small doses. The lamb will be chronically but not seriously weakened by the resulting infection. Lambs in herds with uncrowded, abundant pasture, and those whose mothers can resist or purge infection will obviously be at an advantage.

Nematode eggs will have accumulated to some extent on the pasture by the end of the summer, at which time the lambs are becoming increasingly dependent on grazing rather than suckling. Now, however, the lambs are old enough to begin to develop resistance to infection by gastrointestinal nematodes. The first environmental stresses of autumn and early winter will cause many lambs seriously weakened by nematode burdens, as they would be on crowded pastures, to succumb.

By January the lambs will not have been exposed to new infections of *Ostertagia* and *Nematodirus* for three or four months. As the number of adults of these genera declines (through natural loss) in the lambs, the antigenic stimulus drops and resistance lapses (Donald et al. 1964). Ironically, the lambs which developed resistance to infection late in the previous summer now carry inhibited larvae in the abomasal or intestinal mucosa. In the absence of significant resistance these larvae begin to develop, and during late winter infections of *Ostertagia* and *Nematodirus* begin to appear in lambs, as we observed in this study. If the lambs are severely weakened, as during a particularly severe winter, such infections can have serious consequences. Natural selection has been operating for both resistant hosts and less pathogenic parasites during numerous centuries of winters, however, and many Dall sheep lambs survive in spite of these parasite infections.

CONCLUSIONS

There appears to be a dynamic equilibrium established between Dall sheep and their natural gastrointestinal nematode parasites, such that the most important effect of these parasites is usually to chronically weaken their hosts rather than to directly harm them.

It is lambs, particularly those in their first winter, to which gastrointestinal nematode infections pose the greatest threat.

Among individual Dall sheep at any one time the nematode burden varies considerably, but it rarely approaches levels encountered in domestic sheep.

Acquired resistance may be the most important factor affecting size of the gastrointestinal nematode burden. No indication was found that Dall sheep which were smaller in weight (excluding lambs) or had low marrow fat content, harbored more gastrointestinal nematodes, but larger samples are needed to definitively evaluate these relationships.

The gastrointestinal nematode fauna encountered in *Ovis dalli* has more affinities to that of *O. canadensis*, to which it is phylogenetically more closely related, than to the wild *Ovis* of Europe and central Asia.

Those gastrointestinal nematodes present in the greatest numbers are natural parasites of the Dall sheep. Species are also present which have apparently been accidentally acquired from moose, caribou and bison, but these species are not found in abundance.

An increase in gastrointestinal nematode burdens was observed in lambs during late winter and in peri-parturient ewes in spring. The increase was seen primarily in species of *Nematodirus* and *Ostertagia*.

Marshallagia marshalli was the most common gastrointestinal nematode species found in Dall sheep. It was encountered in moderate numbers in all sheep and its occurrence did not vary with season.

There are indications that four species of *Nematodirus* (*N. davtiani*, *N. archari*, *N. oiratianus* and *N. spathiger*) are physically separated in the small intestine.

MANAGEMENT RECOMMENDATIONS

Dall sheep populations in Alaska should be maintained at levels low enough to avoid crowding and over-utilization of established ranges. Up to a critical point of population density, gastrointestinal nematodes will have little direct effect on the health of sheep although infections chronically weaken them. However, beyond the critical point, although range deterioration may not yet be detectable, the concentration of nematode eggs on pasture will increase logarithmicly as animals reinfect themselves. This will lead not only to weakened adults, but, more seriously, to a drastic decrease in recruitment to the population. Lambs-of-the-year will be lost during the autumn and winter, when heavy loads of larvae attempt to mature in their digestive tract mucosa.

Land use planning should avoid decisions that limit the size of established Dall sheep ranges.

The role of mineral licks in transferring nematode parasite species among subpopulations of sheep should be examined.

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APPENDIX

Gastrointestinal nematodes reported from wild sheep.

A search was made for publications reporting gastrointestinal nematodes found in wild *Ovis* throughout the world. We accumulated numerous references and found reliable reports of the findings from some of the literature we did not actually see, for example as summarized in the Index-Catalogue of Medical and Veterinary Zoology (published annually by the U. S. Department of Agriculture), the Veterinary Bulletin (Commonwealth Bureau of Animal Health, Surrey) or Helminthological Abstracts (Commonwealth Institute of Helminthology, St. Albans). However, in some cases we were unable to obtain either a pertinent publication or to find any information about the findings contained therein, particularly for some of the more obscure Russian publications. Therefore the list of reports which follows is not definitive.

Gastrointestinal nematode species reported for wild *Ovis* in the literature to which we had access are listed below. The list is arranged in sections by nematode group: I. Trichostrongylinae and Haemoncinae, II. Nematodirinae, III. *Skrjabinema* and *Trichuris*, and IV. other nematodes.

Within each group the genera and their species are arranged alphabetically. The various species and subspecies of wild *Ovis* are abbreviated as follows:

Ovis dalli	Abbreviated *O.dalli*
O. canadensis	Abbreviated *O.can.*
O. canadensis canadensis	Abbreviated *O.c.c.*
O. canadensis californiana	Abbreviated *O.c.calif.*
O. canadensis mexicana	Abbreviated *O.c.m.*
O. canadensis nelsoni	Abbreviated *O.c.n.*
O. canadensis texianus	Abbreviated *O.c.t.*
O. nivicola	Abbreviated *O.niv.*
O. ammon	Abbreviated *O.amm.*
O. ammon cycloceros	Abbreviated *O.a.c.*
O. ammon polii	Abbreviated *O.a.p.*
O. ophion	Abbreviated *O.oph.*
O. ophion armeniana	Abbreviated *O.o.a.*
O. vignei	Abbreviated *O.vig.*
O. vignei cycloceros (=O.a.c.)	Abbreviated *O.v.c.*
O. musimon	Abbreviated *O.mus.*

We have found no gastrointestinal nematode reports for *O. orientalis*.

I. Trichostronceylinae and Haemoncinae

Host	Parasite	Location	No. Sheep Exam.	No. Sheep Infected	Reported by
	Cooperia				
O.mus.	*C. curticei*	Europe	?	?	Levine, 1968
O.can.	*C. oncophora*	–	–	–	Yamaguti, 1961
O.c.c.	*C. oncophora*	Montana	12	11	Becklund & Senger, 1967
O.c.c.	*C. oncophora*	Wyoming	?	?	Honess & Winter, 1956
O.mus.	*C. oncophora*	Asia, USSR	?	?	Boev et al., 1963
O.mus.	*C. pectinata*	Austria	?	?	Kutzer & Hinaidy, 1969
O.c.c.	*C. surnabada*	Montana	12	9	Becklund & Senger, 1967
	Haemonchus				
O.can.	*H. contortus*	Wash. D. C. Zoo	?	?	USNM H.C. #3763, 3764*
O.c.c.	*H. contortus*	Wyoming	?	1	Honess & Winter, 1956
O.amm.	*H. contortus*	Asia	?	?	Boev et al., 1963
O.mus.	*H. contortus*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*H. contortus*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*H. contortus*	Czechoslovakia	?	?	Kotrly, 1967
O.c.m.	*H. placei*	New Mexico	9	6	Allen, 1955
	Marshallagia				
O.dalli	*M. marshalli*	Brooks Range	2	1	Rausch, pers. comm.
O.dalli	*M. marshalli*	Mackenzie Mts.	21	2	Simmons, pers. comm.
O.can.	*M. marshalli*	–	–	–	Yamaguti, 1961
O.c.c.	*M. marshalli*	Alberta & B.C.	24	24	Uhazy & Holmes, 1971
O.c.c.	*M. marshalli*	B.C.	43	?	Cowan, 1951
O.c.calif.	*M. marshalli* (ova)	B.C.	2	?	Blood, 1963
O.c.c.	*M. marshalli*	Montana	6	5	Becklund & Senger, 1967
O.c.c.	*M. marshalli*	Montana (bison range)	6	5	Becklund & Senger, 1967
O.c.c.	*M. marshalli*	Montana	1	1	Rush, 1932
O.c.c.	*M. marshalli*	Montana	1	1	Marsh, 1938
O.c.c.	*M. marshalli*	Montana	4	?	Couey, 1950
O.c.c.	*M. marshalli*	Wyoming & Montana	?	?	Dikmans, 1932
O.c.c.	*M. marshalli*	Wyoming & Montana	2	1	Mills, 1937
O.c.c.	*M. marshalli*	Wyoming	?	?	Honess & Winter, 1956
O.c.c.	*M. marshalli*	Idaho	?	?	Quortrup & Sudheimer, 1944
O.c.c.	*M. marshalli*	Colorado	?	?	Spencer, 1943
O.c.c.	*M. marshalli*	S. Dakota	3	3	Boddicker & Hugghins, 1969
O.amm.	*M. marshalli*	USSR	?	?	Boev et al., 1963
O.o.a.	*M. marshalli*	USSR	?	?	Boev et al., 1963
O.mus.	*M. marshalli*	USSR	?	?	Boev et al., 1963
O.niv.	*M. mongolica*	Yakutia	10	10	Gubanov, 1964
O.amm.	*M. mongolica*	Mongolia, USSR	?	?	Boev et al., 1963
O.o.a.	*M. mongolica*	Mongolia, USSR	?	?	Boev et al., 1963
	Mouflonagia				
O.mus.	*M. podjapolskyi*	Germany	26	?	Boch & Honchner, 1962
O.mus.	*M. podjapolskyi*	Crimea	?	?	Levine, 1968
O.c.c.	*Ostertagia* sp.	Colorado	?	?	Spencer, 1943
O.a.p.	*Ostertagia* sp.	Munich Zoo	?	?	Kruger, 1966
O.mus.	*Ostertagia* sp.	Germany	26	?	Boch & Horchner, 1962
O.c.c.	*O. circumcincta*	Alberta & B.C.	24	3	Uhazy & Holmes, 1971
O.c.c.	*O. circumcincta*	B.C.	43	?	Cowan, 1951
O.c.calif.	*O. circumcincta*	B.C.	2	2	Blood, 1963
O.c.c.	*O. circumcincta*	Montana	5	3	Becklund & Senger, 1967

›st	Parasite	Location	No. Sheep Exam.	No. Sheep Infected	Reported by
O.c.c.	*O. circumcincta*	Wyoming	?	?	Honess & Winter, 1956
O.amm.	*O. circumcincta*	USSR	?	?	Boev et al., 1963
O.a.c.	*O. circumcincta*	Turkmenia	?	?	Kibakin et al., 1964
O.o.a.	*O. circumcincta*	USSR	?	?	Boev et al., 1963
O.mus.	*O. circumcincta*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*O. circumcincta*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*O. circumcincta*	Czechoslovakia	?	?	Kotrly, 1967
O.mus.	*O. circumcincta*	Crimea	9	?	Roukhladev, in Ianouchko, 1955
O.mus.	*O. circumcincta*	USSR	?	?	Boev et al., 1963
O.mus.	*O. crimensis*	Crimea	?	?	Levine, 1968
O.mus.	*O. davtiani*	USSR (Armenia)	?	?	Boev et al., 1963
O.mus.	*O. davtiani*	-	-	-	Yamaguti, 1961
O.mus.	*O. gruehneri*	Crimea	9	?	Roukhladev, in Ianouchko, 1955
O.mus.	*O. leptospicularis*	Czechoslovakia	?	?	Kotrly, 1967
O.c.c.	*O. lyrata*	Montana (bison range)	12	3	Becklund & Senger, 1967
O.mus.	*O. lyrata*	USSR	?	?	Boev et al., 1963
O.c.c.	*O. occidentalis*	Alberta & B.C.	24	12	Uhazy & Holmes, 1971
O.c.c.	*O. occidentalis*	B.C.	43	?	Cowan, 1951
O.c.calif.	*O. occidentalis*	B.C.	2	2	Blood, 1963
.c.c.	*O. occidentalis*	Montana	4	?	Couey, 1950
O.c.c.	*O. occidentalis*	Montana	5	3	Becklund & Senger, 1967
O.c.c.	*O. occidentalis*	Wyoming	?	?	Honess & Winter, 1956
O.c.c.	*O. occidentalis*	Idaho	?	?	Dikmans, 1942
O.c.c.	*O. occidentalis*	Idaho	?	?	Quortrup & Sudheimer,1944
O.c.c.	*O. occidentalis*	S. Dakota	3	3	Boddicker & Hugghins,1969
O.amm.	*O. occidentalis*	France, USSR	?	?	Boev et al., 1963
O.o.a.	*O. occidentalis*	USSR	?	?	Boev et al., 1963
O.mus.	*O. occidentalis*	Crimea	9	?	Roukhladev, in Ianouchko, 1955
O.mus.	*O. occidentalis*	USSR	?	?	Boev et al., 1963
O.amm.	*O. orloffi*	USSR	?	?	Boev et al., 1963
O.amm.	*O. orloffi*	Kazakhstan	?	?	Karamendin, 1967
O.c.calif.	*O. ostertagi*	B.C.	2	1	Blood, 1963
O.c.c.	*O. ostertagi*	Montana (bison range)	12	9	Becklund & Senger, 1967
O.c.c.	*O. ostertagi*	Idaho	?	?	(Dikmans, 1942) Becklund & Senger, 1967
O.c.c.	*O. ostertagi*	Idaho	?	?	(Quortrup & Sudheimer, 1944) Becklund & Senger, 1967
O.am.	*O. ostertagi*	Asia	?	?	Boev et al., 1963
O.mus.	*O. ostertagi*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*O. ostertagi*	Asia	?	?	Boev et al., 1963
O.can.	*O. trifurcata*	Montana ?	?	?	USNM H.C. #46224*
O.c.c.	*O. trifurcata*	Wyoming	?	?	Honess & Winter, 1956
O.am.	*O. trifurcata*	USSR	?	?	Boev et al., 1963

Host	Parasite	Location	No. Sheep Exam.	No. Sheep Infected	Reported by
O.vig.	*O. trifurcata*	Kazakhstan	3	?	Boev, Laurov et al. 1957 as cited by Gvozdev, 1968
O.mus.	*O. trifurcata*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*O. trifurcata*	Czechoslovakia	?	?	Kotrly, 1967
O.mus.	*O. trifurcata*	Crimea	9	?	Roukhladev, in Ianouchko, 1955
O.mus.	*O. trifurcata*	USSR	?	?	Boev et al., 1963
	Pseudostertagia				
O.c.c.	*P. bullosa*	Colorado	?	?	Pillmore, 1961
O.c.m.	*P. bullosa*	New Mexico	9	4	Allen, 1955
	Skrjabinagia				
O.mus.	*S. kolchida*	Austria	?	?	Kutzer & Hinaidy, 1969
	Spiculopteragia				
O.mus.	*S. bohmi*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*S. spiculoptera*	Crimea	9	?	Roukhladev, in Ianouchko, 1955
O.c.c.	*Trichostrongylius* sp.	Montana (bison range)	12	5	Becklund & Senger, 1967
O.a.p.	*Trichostrongylius* sp.	Munich Zoo	?	?	Kruger, 1966
O.can.	*T. axei*	Wash. D.C. Zoo	?	?	USNM H.C. #3762, 31384*
O.can.	*T. axei*	–	–	–	Levine, 1968
O.mus.	*T. axei*	–	–	–	Levine, 1968
O.mus.	*T. axei*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*T. axei*	Czechoslovakia	?	?	Kotrly, 1967
O.mus.	*T. axei*	USSR	?	?	Boev et al., 1963
O.mus.	*T. capticola*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*T. capticola*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*T. capticola*	Czechoslovakia	?	?	Kotrly, 1967
O.can.	*T. columbiformis*	Wash. D.C. Zoo	?	?	USNM H.C. #31385*
O.amm.	*T. columbiformis*	USSR	?	?	Boev et al., 1963
O.oph.	*T. columbiformis*	USSR	?	?	Boev et al., 1963
O.mus.	*T. columbiformis*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*T. columbiformis*	Czechoslovakia	?	?	Kotrly, 1967
O. amm.	*T. probolurus*	Central Asia	?	?	Boev et al., 1963
O.o.a.	*T. probolurus*	Central Asia	?	?	Boev et al., 1963
O.can.	*T. rugatus*	Wash. D.C. Zoo	1	1	Price, 1930
O.o.a.	*T. skrjabini*	USSR	?	?	Boev et al., 1963
O.o.a.	*T. vitrinus*	Asia	?	?	Boev et al., 1963
O.mus.	*T. vitrinus*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*T. vitrinus*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*T. vitrinus*	Asia	?	?	Boev et al., 1963
II. Nematodirinae					
O.dalli	*Nematodirus* sp.	Mackenzie Mts.	21	17	Simmons, pers. comm.
O.c.calif.	*Nematodirus* sp. (ova)	B.C.	2	?	Blood, 1963
O.c.c.	*Nematodirus* sp.	Montana	15	?	Couey, 1950
O.c.c.	*Nematodirus* sp.	Montana	1	1	Capelle, 1966
O.c.c.	*Nematodirus* sp.	S. Dakota	3	1	Boddicker & Hugghins, 1969

.t	Parasite	Location	No. Sheep Exam.	No. Sheep Infected	Reported by
O.c.calif.	*Nematodirus* sp.	California	?	1 adult	McCullough & Schneegas, 1966
O.c.calif.	*Nematodirus* sp.	California	9	7 lambs	McCullough & Schneegas, 1966
O.v.c.	*Nematodirus* sp.	Munich Zoo	?	?	Kruger, 1966
O.c.c.	*N. abnormalis*	Wyoming	?	?	Honess & Winter, 1956
O.amm.	*N. abnormalis*	Asia	?	?	Boev et al., 1963
O.o.a.	*N. abnormalis*	Asia	?	?	Boev et al., 1963
O.vig.	*N. abnormalis*	west Tyan-Shan	3	?	Boev, Lavrov et al, 1957 as cited by Gvozdev, 1968
O.c.c.	*N. archari*	Alberta & B.C.	25	21	Uhazy & Holmes, 1971
O.c.c.	*N. archari*	Montana	6	4	Becklund & Senger, 1967
O.amm.	*N. archari*	USSR	?	?	Boev et al., 1963
O.amm.	*N. archari*	Kazakhstan	15	?	Sokolova, 1948
O.amm.	*N. archari*	Kazakhstan	?	?	Karabaev, 1953
O.c.c.	*N. davtiani*	Alberta & B.C.	25	13	Uhazy & Holmes, 1971
O.c.c.	*N. davtiani*	Montana	?	?	Becklund, 1966
O.c.c.	*N. davtiani*	Montana	6	1	Becklund & Senger, 1967
O.amm.	*N. dogieli*	USSR	?	?	Boev et al., 1963
O.amm.	*N. dogieli*	Kazakhstan	?	?	Karabaev, 1953
O.o.a.	*N. dogieli*	USSR	?	?	Boev et al., 1963
O.o.a.	*N. dogieli*	Armenia	-	-	Yamaguti, 1961
O.c.c.	*N. filicollis*	Alberta	43	?	Cowan, 1951
O.a.c.	*N. filicollis*	Turkmenia	?	?	Kibakin et al., 1964
mus.	*N. filicollis*	Germany	26	?	Boch & Horchner, 1962
..mus.	*N. filicollis*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*N. filicollis*	Czechoslovakia	?	?	Kotrly, 1967
O.c.c.	*N. helvetianus*	Montana	12	4	Becklund & Senger, 1967
O.a.c.	*N. helvetianus*	Turkmenia	?	?	Kibakin et al., 1964
O.c.c.	*N. maculosus*	Alberta & B.C.	25	1	Uhazy & Holmes, 1971
O.c.c.	*N. odocoilei*	Montana	12	5	Becklund & Walker, 1967a
O.c.c.	*N. oiratianus*	Alberta & B.C.	25	16	Uhazy & Holmes, 1971
O.c.c.	*N. oiratianus*	Montana	6	6	Becklund & Senger, 1967
O.c.c.	*N. oiratianus*	Colorado	?	?	Pillmore, 1961
O.niv.	*N. oiratianus*	Yakutia	10	10	Gubanov, 1964
O.amm.	*N. oiratianus*	USSR, Mongolia	?	?	Boev et al., 1963
O.c.c.	*N. spathiger*	Alberta & B.C.	25	3	Uhazy & Holmes, 1971
O.c.c.	*N. spathiger*	Montana	12	11	Becklund & Senger, 1967
O.c.c.	*N. spathiger* (ova)	Montana	1	1	Forrester & Hoffman, 1963
O.c.c.	*N. spathiger*	Wyoming	?	1	Honess & Winter, 1956
O.c.c.	*N. spathiger*	Colorado	?	?	Pillmore, 1961
O.c.t.	*N. spathiger*	New Mexico	1	1	Allen & Kennedy, 1952
O.can.	*N. spathiger*	Wash. D.C. Zoo	?	?	USNM H.C. #38936*
O.amm.	*N. spathiger*	USSR	?	?	Boev et al., 1963
O.o.a.	*N. spathiger*	USSR	?	?	Boev et al., 1963
O.mus.	*N. spathiger*	Czechoslovakia	?	?	Kotrly, 1967
O.mus.	*N. spathiger*	USSR	?	?	Boev et al., 1963
	Nematodirella				
O.a.c.	*N. longisimespiculata* sp. *gazelli*	Turkmenia	?	?	Kibakin et al., 1964

III. *Skrjabinema* and *Trichuris*

Host	Parasite	Location	No. Sheep Exam.	No. Sheep Infected	Reported by
O.can.	*Skrjabinema* sp.	Utah	?	?	Wilson & Honess, 1965
O.c.calif.	*Skrjabinema* sp.	B.C.	2	1	Blood, 1963
O.c.t.	*Skrjabinema* sp.	New Mexico	1	1	Allen & Kennedy, 1952
O.c.m.	*Skrjabinema* sp.	Arizona	12	?	Allen & Erling, 1964
O.dalli	*S. ovis*	Mackenzie	21	19(?)	Simmons, pers. comm.
O.can.	*S. ovis*	Colorado, Idaho, Montana, N. Mexico	?	5	Schad, 1959
O.c.c.	*S. ovis*	Alberta & B.C.	25	2	Uhazy & Holmes, 1971
O.c.c.	*S. ovis*	Colorado	?	?	Olsen & White, 1949
O.c.c.	*S. ovis*	S. Dakota	3	1	Boddicker & Hugghins, 1969
O.c.n.	*S. ovis*	Nevada	4	3	Allen, 1964
O.c.t.	*S. ovis*	New Mexico	9	8	Allen, 1955
O.a.c.	*S. ovis*	Turkmenia	?	?	Kibakin et al., 1964
O.niv.	*S. ovis*	Yakutia	10	10	Gubanov, 1964
O.mus.	*S. ovis*	Austria	?	?	Kutzer & Hinaidy, 1969
O.dalli	*Trichuris* sp.	Mackenzie Mts.	21	15	Simmons, pers. comm.
O.can.	*Trichuris* sp.	Wash. D.C. Zoo	?	?	USNM H.C. #29190, 56896
O.c.c.	*Trichuris* sp. (ova)	Montana	15	?	Couey, 1950
O.c.c.	*Trichuris* sp.	Idaho	?	?	Quortrup & Sudheimer, 1944
O.c.t.	*Trichuris* sp.	New Mexico	1	1	Allen & Kennedy, 1952
O.mus.	*T. capreoli*	Austria	?	?	Kutzer & Hinaidy, 19
O.c.calif.	*T. discolor*	B.C.	2	1	Blood, 1963
O.c.n.	*T. discolor*	Nevada	4	2	Allen, 1964
O.c.t.	*T. discolor*	New Mexico	9	8	Allen, 1955
O.mus.	*T. globulosa*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*T. globulosa*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*T. globulosa*	Czechoslovakia	?	?	Kotrly, 1967
O.c.c.	*T. ovis*	Wyoming	?	1	Honess & Winter, 1956
O.c.c.	*T. ovis*	S. Dakota	3	1	Boddicker & Hugghins, 1969
O.a.c.	*T. ovis*	Turkmenia	?	?	Kibakin et al., 1964
O.mus.	*T. ovis*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*T. ovis*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*T. ovis*	Paris Zoo	?	?	Nouvel et al., 1968
O.mus.	*T. ovis*	Czechoslovakia	?	?	Kotrly, 1967
O.mus.	*T. ovis*	Crimea	9	9	Roukhladev in Ianouchko, 1955
O.c.c.	*T. schumakovitschi*	Alberta & B.C.	25	17	Uhazy & Holmes, 1973
O.niv.	*T. skryabini*	Yakutia	10	9	Gubanov, 1964
O.a.c.	*T. skryabini*	Turkmenia	?	?	Kibakin et al., 1964
O.o.a.(?)	*T. skryabini*	Azerbaidzhan	?	?	Gusienov & Asadova, 1966
O.mus.	*T. skryabini*	Germany	26	?	Boch & Horchner, 1962

IV. Other Nematodes

Host	Parasite	Location	No. Sheep Exam.	No. Sheep Infected	Reported by
	Bunostorum				
O.mus.	*B. trigonocephalum*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*B. trigonocephalum*	Austria	?	?	Kutzer & Hinaidy, 1969

ɔst	Parasite	Location	No. Sheep Exam.	No. Sheep Infected	Reported by
O.dalli	*Capillaria* sp.	Mackenzie Mts.	21	1	Simmons, pers. comm.
O.c.c.	*Capillaria* sp.	Alberta	25	1	Uhazy & Holmes, 1971
O.mus.	*C. bovis*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*C. bovis*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*C. bovis*	Czechoslovakia	?	?	Kotrly, 1967
	Chabertia				
O.amm.	*C. ovina*	Turkmenia	?	?	Kibakin et al., 1964
O.mus.	*C. ovina*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*C. ovina*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*C. ovina*	Czechoslovakia	?	?	Kotrly, 1967
O.c.m.	*Oesophagostomum* sp. (larva)	New Mexico	9	1	Allen, 1955
O.a.c.	*O. columbianum*	Turkmenia	?	?	Kibakin et al., 1964
O.can.	*O. venulosum*	Wash. D.C. Zoo	?	?	USNM H.C. #56895*
O.mus.	*O. venulosum*	Germany	26	?	Boch & Horchner, 1962
O.mus.	*O. venulosum*	Austria	?	?	Kutzer & Hinaidy, 1969
O.mus.	*O. venulosum*	Czechoslovakia	?	?	Kotrly, 1967
	Strongyloides				
O.mus.	*S. papillosus*	Austria	?	?	Kutzer & Hinaidy, 1969

* Cited by Becklund and Senger 1967, as occurring in the U.S. National Museum's Helminthological Collection.