

# Seasonal prevalence of gastrointestinal nematodes of beef calves grazed on irrigated pastures in the lower Sacramento Valley of California

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## SUMMARY

Two worm-free calves were allowed to graze on irrigated pasture with a naturally infected herd for each of 34 one-month periods from November 1979 to August 1982. After each grazing period, the calves were transferred to a cement-floored pen for 3 weeks and then were euthanatized and necropsied.

*Ostertagia ostertagi* and *Cooperia oncophora* were the most prevalent species of nematodes recovered. Adults and larvae of *Ostertagia* spp and *Cooperia* spp were most numerous in winter and spring and least numerous during summer. The proportions of *Ostertagia* spp that were inhibited as fourth-stage larvae increased in late fall, peaked from March through April, and then decreased to low values during summer. The maximal inhibition in 1980, 1981, and 1982 was 72, 65, and 62%, respectively. The number of larval *Cooperia* spp was highest in winter months and, except for one grazing period when 55% of the *Cooperia* spp were larvae, the total numbers represented < 15% of the nematode population during all grazing periods. Other nematodes encountered were *Trichostrongylus axei*, *Haemonchus* spp, *O lyrata*, and *O occidentalis* in the abomasum; *C surnabata*, *C punctata*, *Nematodirus helvetianus*, *T colubriformis*, and *Bunostomum phlebotomum* in the small intestine; and *Oesophagostomum venulosum* and *Trichuris ovis* in the large intestine.

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The importance of obtaining qualitative data on seasonal transmission and other epidemiologic aspects in the prevention and control of parasitic gastroenteritis of ruminants has been well documented in recent reviews.<sup>1-4</sup> These studies emphasized knowledge of seasonality of individual species of parasites as mature forms and as inhibited larvae. In addition to establishing qualitative epidemiologic patterns, it also was essential that the de-

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gree to which the pattern may vary in quantitative manner from year to year be established.

In the United States, the epidemiologic features of parasites of ruminants in different climatic regions is not completely known. In many regions where qualitative studies have revealed seasonal patterns, the quantitative variation in the epidemiologic variables from one year to the next has not been evaluated.

The study reported here represents 34 months of qualitative and quantitative observations of the epidemiologic features of helminth parasites in beef calves grazing on irrigated pasture in the lower Sacramento Valley of California.

## Materials and Methods

During the period November 1979 through August 1982, the study was conducted on a commercial ranch 20 miles southeast of Dixon, Calif. The pasture was a typical improved irrigated pasture. Forage was composed mainly of annual clover and grasses. Irrigation was achieved by flooding between borders every 10 days to 2 weeks during summer months. Less-frequent irrigation was done during spring and fall months. The contaminant cattle in the field during the trial were stocker steers, largely of Hereford and Angus breeding. The steers were placed on the pasture when weaned (200 to 230 kg) and remained there until they reached feedlot weight (290 to 350 kg). A small flock (50 to 100) of sheep shared the pasture.

**Tracer calves**—Sixty-eight Holstein steer calves raised under essentially worm-free conditions, weighing  $182.2 \pm 61.6$  kg (mean  $\pm$  SD), were used in the study to determine pasture infectivity. Before grazing began, all tracer calves had fecal egg counts of 0 (by flotation method). Nevertheless, all were treated with levamisole (8 mg/kg of body weight) 7 days before grazing began. Two worm-free calves were placed on the pasture and were allowed to graze with cattle already at the ranch. After approximately 30 days, the calves were replaced by another pair of worm-free calves. Tracer calves removed from pasture were brought to the Animal Research Service of the University of California at Davis. They were kept in dry lots with concrete floors and were maintained essentially free of helminth exposure for 3 weeks, at which time they were euthanatized and necropsied.

At necropsy, the abomasum, small intestine, and large intestine were removed. Ten percent aliquots of abomasal and small intestinal contents were fixed in formalin (10% final concentration) and were stored for later examination.

The abomasal and small intestinal mucosae were soaked separately in saline solution overnight at 37 C. After soaking, the saline solution was set aside, and the abomasal and small intestinal mucosae were washed separately with water. Mucosal washings were added to the appropriate saline solution, which then was passed through a wire sieve of 75- $\mu$ m aperture (Tyler

TABLE 1—Species and prevalence of gastrointestinal nematodes of all stages found in three organ sites of 68 tracer calves

Organ	Species	Prevalence
Abomasum	<i>Ostertagia ostertagi</i>	98.5
	<i>Trichostrongylus axei</i>	83.8
	<i>Haemonchus</i> spp	54.4
	<i>O. lyrata</i>	5.9
	<i>O. occidentalis</i>	2.9
Small intestine	<i>Cooperia oncophora</i>	95.6
	<i>C. surnabata</i>	86.4
	<i>Nematodirus helvetianus</i>	73.5
	<i>T. colubriformis</i>	27.9
	<i>C. punctata</i>	17.6
	<i>Bunostomum phebotoomum</i>	1.5
Large intestine	<i>Oesophagostomum venulosum</i>	35.3
	<i>Trichuris ovis</i>	26.5

equivalent, 200 mesh). The retained material was fixed in 10% formalin.

Total worm counts in aliquots of abomasal and small intestinal contents were estimated after washing on a 75- $\mu$ m aperture sieve. The material retained on the sieve was collected and was brought to a volume of 1,000 ml. With constant stirring, two 50-ml aliquots were taken, and all helminths in each aliquot were counted and identified. When < 100 worms were counted, additional aliquots were taken until at least 100 worms were counted and were identified, or until the entire 1,000 ml was examined. Worms in the material obtained from the soaking of the abomasal and small intestinal mucosae were counted in the same manner as those in the abomasal and small intestinal contents.

Contents of the large intestine were emptied into a bucket. The entire contents were washed in small amounts on a wire screen with aperture of 850  $\mu$ m (Tyler equivalent, 20 mesh). After all contents were washed, the material that remained on the screen was fixed in formalin. The entire contents were examined, and worms were counted visually.

The number of nodules in the wall of the small intestine attributed to the *Oesophagostomum* spp larvae was estimated by palpation of the entire organ.

For analysis of data, the month in which the median point of the grazing period occurred was considered as the grazing month. Grazing periods were assigned to seasons according to the month of grazing (September through November, fall; December through February, winter; March through May, spring; and June through August, summer). Climatologic data were obtained from a monthly publication of the US Government.<sup>a</sup>

## Results

Gastrointestinal nematodes were found in all tracer calves. *Ostertagia ostertagi* and *Cooperia oncophora* were the most prevalent species in the abomasum and small intestine, respectively. The genera and species found, as well as their prevalences and host sites, are given in Table 1. Seasonal and annual variations in the extent and composition of the nematode populations were observed. The total worm count in the tracer calves was greatest during winter and spring grazing periods, as were adults and larvae of *Ostertagia* spp and *Cooperia* spp. Smallest numbers were found during the summer (Table 2). The proportions of inhibited fourth-stage larvae (L4) of *Ostertagia* spp increased in late fall, peaked from March through April, and decreased to low values during the summer (Fig 1). *Cooperia* spp larval stages remained low during

<sup>a</sup> Climatological Data—California, National Oceanic and Atmospheric Administration, Department of Commerce, United States.

most of the study (Table 2); however during winter months, they increased and in one grazing period (Dec 26, 1979, through Feb 5, 1980), larvae constituted 55% of the *Cooperia* population (Table 2).

Numbers of large intestinal nematodes were small, compared with those in the abomasum and small intestine. Mean burdens of gastrointestinal nematodes for each host organ during different seasons of the year are given in Table 3.

Although a large proportion of calves was infected with *Trichostrongylus* spp (*T. axei* and *T. colubriformis*), *Nematodirus helvetianus*, *Haemonchus* spp, and *Trichuris ovis* (Table 1), these parasites were found in low numbers (Table 3).

*Oesophagostomum venulosum* was the only species of this genus that was recovered. The prevalence of mature *Oe. venulosum* in the lumen of the large intestine and of nodules in the small intestine during the 4 seasons of the year are given in Table 3. *Bunostomum phlebotomum* was recovered from only 1 calf.

Exsheathed parasitic third-stage larvae (L3) of *Nematodirus* spp were recovered from the small intestine of 18 (26%) of the calves. Infected calves harbored a mean of 32 larvae/calf (range, 2 to 143). These larvae were cylindrical, with a mean total length of  $1.28 \pm 0.68$  mm and a tail composed of 3 triangular projections (Fig 2 and 3).

Larvae classified as immature *Cooperia* spp (Table 2) measured  $1.86 \pm 0.27$  mm (range, 1.10 to 2.72 mm) in length. They had larval tail morphologic features similar to those of the parasitic L3 of *C. punctata* described by Stewart<sup>5</sup> and used by Douvres<sup>6</sup> in a key for identification of parasitic L3 of *Cooperia* spp (Fig 4). In addition, larvae with tail morphology similar to that of *C. oncophora*, collected 3 days after infection<sup>7</sup> (Fig 5), were seen among the examined specimens. A provisional buccal capsule, along with cuticular inflation and transverse cuticular striations in the cephalic region (Fig 6), similar to that of the L4 of *C. pectinata*<sup>8</sup> and considered distinctive of the L4 by Douvres,<sup>6</sup> was observed in most of these worms. On the basis of these findings, we concluded that a mixture of exsheathed parasitic late L3 and early L4 were in the necropsied calves.

The monthly totals of evaporation and rainfall, and the monthly means of minimal, mean, and maximal daily temperatures during the study are given in Figures 7 and 8, respectively.

## Discussion

The species of gastrointestinal nematodes found in calves of this study generally were similar to those reported previously in California.<sup>9-11</sup> *Ostertagia* spp and *Cooperia* spp, those nematodes with the highest prevalence in this study (Table 1), also had the highest prevalence in previous studies of cattle in the Sacramento Valley,<sup>9</sup> the California Sierra foothills,<sup>10</sup> and the California high sierra region.<sup>11</sup>

Although pasture transmission of infective larvae of these 2 genera took place during the entire study period, it was detected in markedly different numbers during the 4 seasons. Maximal numbers were found from late winter to early spring, but decreased in late spring and were low in summer (Tables 2 and 3). These observations agreed with those of studies, using analogous methods<sup>9-11</sup> and

TABLE 2—Total numbers of gastrointestinal nematodes found in the abomasum, small intestine, and large intestine of 68 calves during each of 34 grazing periods in the lower Sacramento Valley

Grazing period	Abomasum			Small intestine			Large intestine‡ Total No. of worms
	Total No. of worms	<i>Ostertagia</i> spp		Total No. of worms	<i>Cooperia</i> spp		
		Adults	EL4*		Adults	Immature†	
<b>1979</b>							
11/21 to 12/24	25,819	22,983	1,111	14,639	14,640	0	176
12/26 to 2/5/80	29,671	26,081	20,914	7,918	3,567	4,352	66
<b>1980</b>							
2/5 to 3/5	44,543	26,796	15,345	14,050	13,670	370	39
3/5 to 4/9	20,130	4,642	14,443	19,367	13,046	408	4
4/9 to 5/5	474	237	210	4,089	2,348	16	0
5/5 to 6/2	476	207	130	1,203	869	15	0
6/2 to 7/2	114	22	4	216	162	0	0
7/2 to 8/6	430	139	0	572	405	0	4
7/29 to 9/3	651	438	2	973	897	17	5
9/3 to 9/30	454	358	0	794	763	1	0
9/30 to 10/28	4,329	3,863	18	4,616	4,443	135	1
10/28 to 11/26	8,111	7,688	0	14,080	13,908	35	2
11/26 to 12/22	13,256	12,814	171	24,918	24,424	492	3
<b>1981</b>							
12/22/80 to 1/19/81	3,722	3,613	25	5,919	5,742	8	6
1/19 to 2/18	21,141	15,586	4,730	40,319	37,181	2,919	6
2/18 to 3/20	64,847	27,837	36,580	35,812	33,401	1,220	4
3/20 to 4/15	8,859	2,848	5,779	10,812	9,096	1,476	0
4/15 to 5/14	3,360	963	2,241	13,906	13,132	258	0
5/14 to 6/12	840	580	185	8,809	2,117	2	0
6/12 to 7/8	112	86	0	5,490	1,956	0	0
7/8 to 8/5	90	60	0	69	0	61	0
8/5 to 8/31	70	65	0	512	393	5	0
8/31 to 9/29	994	889	1	1,177	1,096	33	1
9/29 to 10/23	2,751	2,634	14	11,174	10,776	41	0
10/23 to 11/19	7,933	7,716	0	15,657	14,671	339	5
11/19 to 12/17	60,700	49,803	7,613	32,900	32,900	0	0
<b>1982</b>							
12/17/81 to 1/14/82	102,849	67,098	32,658	70,205	66,102	4,052	19
1/14 to 2/16	41,600	30,004	11,485	42,562	37,142	4,520	0
2/16 to 3/15	20,946	14,765	6,117	62,672	58,266	2,558	0
3/15 to 4/13	28,197	10,576	17,507	5,526	5,311	140	15
4/13 to 5/11	7,634	3,568	3,422	4,919	4,041	185	0
5/11 to 6/8	18	10	8	314	48	0	0
6/8 to 7/15	1,258	983	5	2,037	875	9	0
7/15 to 8/17	84	29	0	220	164	0	0

\* EL4 = Early fourth-stage larvae. † Includes exsheathed third-stage larvae, EL4, and late fourth-stage larvae. ‡ Includes cecum.

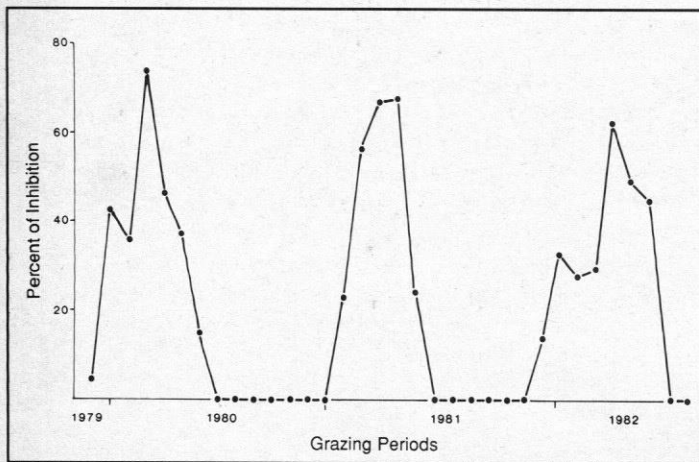


Fig 1—Mean monthly percentages of inhibited fourth-stage larvae of *Ostertagia* spp recovered from the abomasum of 68 calves in the Sacramento valley of California.

using different methods,<sup>12,b</sup> in locations close to where this study was conducted. Weather conditions (Fig 7 and 8) from November to May appeared to be optimal for lar-

<sup>b</sup> Miller JE, *Epidemiology and economics of strongylate nematode parasites of the bovine in central California*. PhD dissertation. University of California, Davis, 1983.

TABLE 3—Mean numbers of abomasal, small intestinal, and large intestinal nematodes per calf during different seasons

Nematodes	Fall	Winter	Spring	Summer
Total nematodes	12,013	70,078	22,825	1,621
Abomasum	4,096	38,425	13,484	351
Small intestine	7,916	31,611	9,338	1,269
Large intestine	1	32	3	1
Total <i>Ostertagia</i> spp	3,873	37,404	13,264	230
Adult	3,858	26,954	5,147	228
Early L4	6	10,017	8,050	1
% of total early L4	0.1	22.0	60.7	0.4
Total <i>Cooperia</i> spp	7,707	31,290	8,613	618
Adult	7,609	29,363	8,241	606
Larvae	97	1,927	372	12
% larvae	1.2	6.1	4.3	1.9
Other nematodes*				
<i>Nematodirus helvetianus</i>	208	295	701	650
<i>Trichostrongylus</i> spp	129	975	228	60
<i>Haemonchus</i> spp	95	72	16	62
<i>Trichuris ovis</i>	0	8	2	1
<i>Oesophagostomum venulosum</i>	1	24	1	0
<i>Oesophagostomum</i> spp nodules	29	13	1	22

\* Includes adults and larvae.  
L4 = fourth-stage larvae.

val development and/or survival. The high evaporation rates and ambient temperatures of summer accounted for the low transmission rate observed during that period.<sup>b</sup>

The results of this study and the work of others suggest that infections acquired in winter originated from eggs

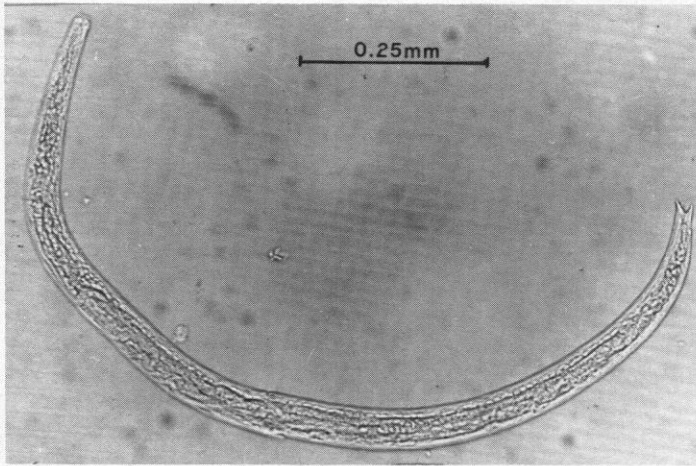


Fig 2—*Nematodirus* spp exsheathed parasitic third-stage larva.

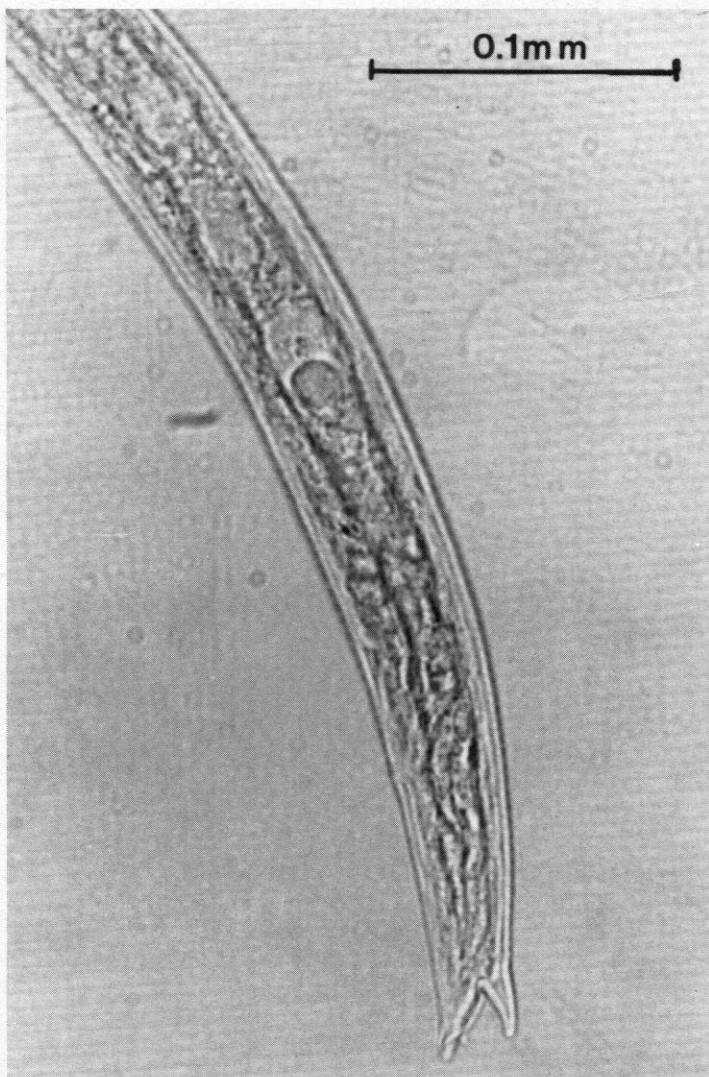


Fig 3—Tail region of *Nematodirus* spp exsheathed parasitic third-stage larva.

deposited in fall. The survival of strongylid nematode eggs in fecal pats during summer months in the Sacramento Valley is low.<sup>12,b</sup> The source of fall contamination was considered to be (1) eggs produced by worms, larvae of

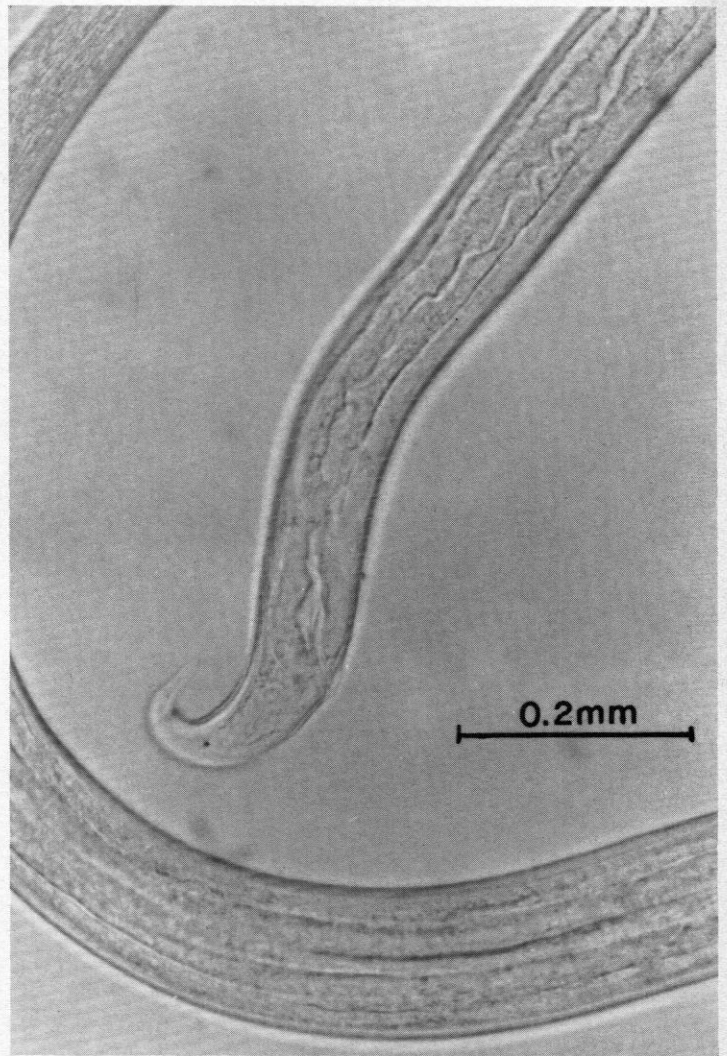


Fig 4—Tail region of *Cooperia* spp exsheathed parasitic third-stage larva.

which remained inhibited during summer and then developed to maturity during late summer and early fall, (2) the small population of adults maintained by the low level of infection from pasture, and (3) maturation of inhibited larvae during the summer months. Spring infection probably resulted from overwintering larvae and from eggs deposited in the winter and spring.

*Ostertagia* inhibited larvae (Tables 2 and 3; Fig 1) were found in low numbers in tracer calves by late fall, peaked from late winter to early spring, and then decreased as did the number of infective larvae on pasture in late spring and summer. This pattern of larval inhibition and development agreed with that of previous studies in sun belt states.<sup>9-14</sup>

The simultaneous finding of mature worms and inhibited larvae (Tables 2 and 3; Fig 1) in tracer calves during winter months reflected different developmental tendencies in the larval population on pasture. These developmental tendencies may result from environmental influences, from genetic makeup, or from other unknown factors.<sup>15,16</sup> The inhibition of larvae in calves from December to February may result from "cold conditioning," as described by Michel et al.<sup>17</sup> During fall months, tem-

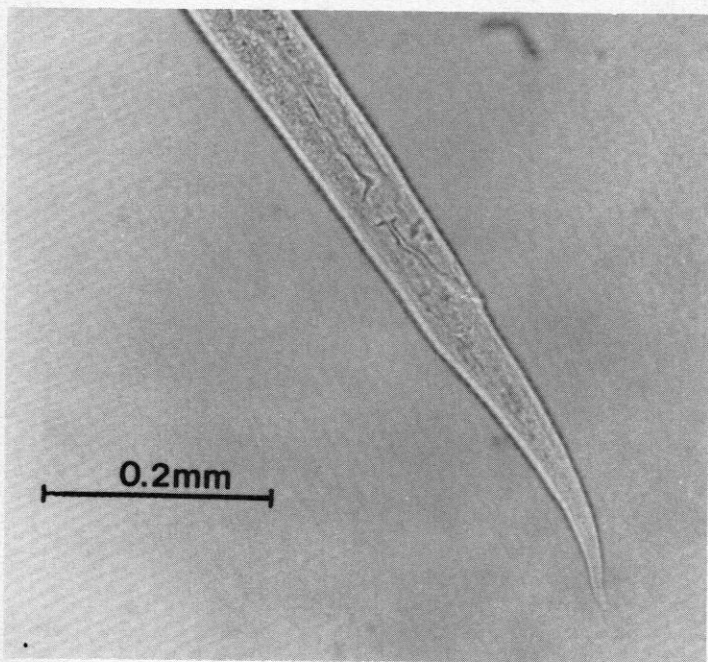


Fig 5—Tail region of *Cooperia* spp exsheathed parasitic third-stage larva.

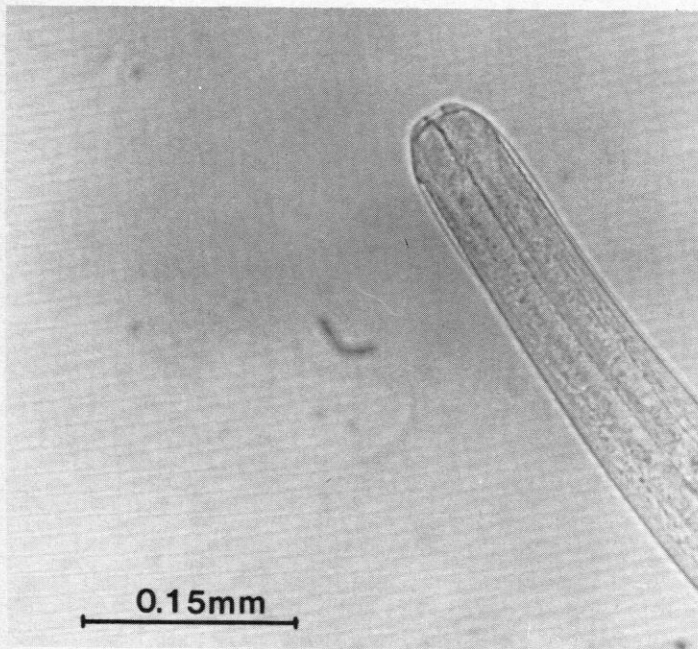


Fig 6—Provisional buccal capsule of *Cooperia* spp early fourth-stage larva.

peratures decrease, reaching their lowest extremes from December to February (Fig 8). This temperature decrease is not markedly different from the one that precedes fall larval inhibition in northern temperate regions, where peak inhibition develops during the fall months.<sup>13</sup> Whether all inhibited larvae arose from overwintered infective larvae could not be determined by the experimental design used in this study.

The maximal percentage of inhibited *Ostertagia* larvae in tracer calves was quite constant from one year to the next, even though the total numbers of *Ostertagia* spp varied to a large degree (Table 2; Fig 1). This same relationship was observed in a study of calves in the Sierra foothills,<sup>10</sup> where frequent use of anthelmintics active only

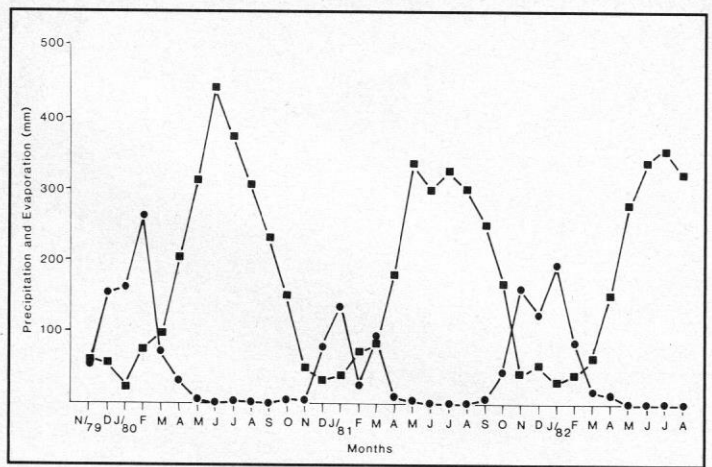


Fig 7—Total monthly evaporation (■) and rainfall (●) in millimeters between November 1979 and August 1982.

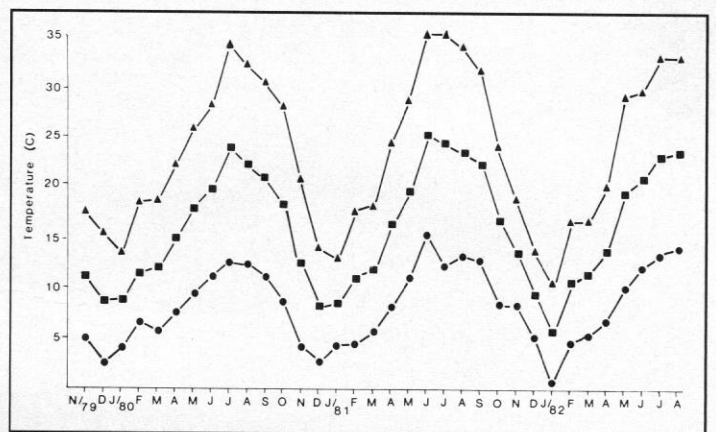


Fig 8—Monthly means of minimal daily temperatures (●), mean daily temperatures (■), and maximal daily temperatures (▲) between November 1979 and August 1982.

against mature stages may have selected for strains that were genetically prone to inhibition. Results of this study do not support that hypothesis, because regular use of anthelmintics had not been a management practice on the ranch of this report.

Our results suggested that type-I ostertagiosis may develop in California, as it does in all sun belt states, from late fall to early spring, pretype II may develop from midspring to late summer, and type II may develop from late summer to fall. The importance of these findings, relative to the prevention of ostertagiosis in cattle, has been discussed.<sup>4,9,13</sup>

In this study, the source of exsheathed parasitic L3 of *Nematodirus* spp and *Cooperia* spp was unclear. Although the pens, in which tracer calves were kept, were washed frequently, contamination can not be excluded as a possible source. Nevertheless, despite a previous report,<sup>15</sup> *Nematodirus* spp and *Cooperia* spp, in some instances, may be inhibited at the L3 stage. In this regard, arrestment of development of *Trichostrongylus* spp as the exsheathed parasitic L3 and *Haemonchus contortus* as the sheathed L3 has been observed in sheep.<sup>2,15,18-20</sup>

There is great morphologic variation in the tail of the larvae of genus *Nematodirus*.<sup>21-25</sup> On the basis of tail morphologic features, the larvae found in the examined

calves may not have been *N. helvetianus*.<sup>23</sup> Tail morphologic features of these larvae resembled those of *N. filicollis*<sup>22,24</sup> and *N. abnormalis*.<sup>25</sup> Although these species are found commonly in sheep in the United States, *N. abnormalis* has not been reported as a parasite of cattle, and *N. filicollis*, considered a parasite of cattle as well as sheep, has not been reported from cattle in the United States.<sup>26</sup> This raises the possibility that the source of *Nematodirus* larvae may have been ruminants other than cattle. During the course of the study, a small band of sheep (50 to 100) was grazed on the pasture. At no time were other ruminants kept in the pens at the University of California. Thus, if the *Nematodirus* larvae were species originating from sheep, they must have been ingested while calves were on the pasture 3 to 4 weeks before necropsy. This raises a further question regarding the developmental pattern of species other than *N. helvetianus* in cattle.

Although the number of calves infected by *Oe venulosum* and the number of parasites recovered from each calf were low (Tables 1 and 3), it was the only species of this genus recovered from the cecum and large intestine. These findings agreed with the suggestion of Baker and Fisk<sup>10</sup> that *Oe venulosum* may replace *Oe radiatum* in western United States and that a seasonality of uninhibited and inhibited development may be associated with this host-parasite-environmental complex.

## References

1. Michel JF. The epidemiology and control of some nematode infections of grazing animals. *Adv Parasitol* 1969;7:211-281.
2. Michel JF. The epidemiology and control of some nematode infections in grazing animals. *Adv Parasitol* 1976;14:355-397.
3. Michel JF. Epidemiology and control of gastrointestinal helminths in domestic animals. In: Vanden Bossche H, Thienport D, Janssens PG, eds. *Chemotherapy of gastrointestinal helminths*. Heidelberg, Berlin: Springer-Verlag, 1985;67-123.
4. Armour J. The epidemiology of helminth disease in farm animals. *Vet Parasitol* 1980;6:7-46.
5. Stewart TB. The life history of *Cooperia punctata*, a nematode parasitic in cattle. *J Parasitol* 1954;40:321-327.
6. Douvres FW. Keys to the identification and differentiation of the immature parasitic stages of gastrointestinal nematodes of cattle. *Am J Vet Res* 1957;18:81-85.
7. Isenstein RS. The life history of *Cooperia oncophora* (Railliet, 1898) Ransom, 1907, a nematode parasite of cattle. *J Parasitol* 1963;49:235-240.
8. Keith RK. The life history of *Cooperia pectinata* Ransom. *Aust J Zool* 1967;15:739-744.
9. Baker NF, Fisk RA, Bushnell RB, et al. Seasonal occurrence of infective larvae on irrigated pasture grazed by cattle in California. *Am J Vet Res* 1981;42:1188-1191.
10. Baker NF, Fisk RA. Seasonal occurrence of infective nematode larvae in California Sierra foothill pastures grazed by cattle. *Am J Vet Res* 1986;47:1680-1685.
11. Baker NF, Fisk RA, Rimbe CW. Seasonal occurrence of infective nematode larvae in California High Sierra pastures grazed by cattle. *Am J Vet Res* 1984;45:1393-1397.
12. Furman DP. Effects of environment upon the free-living stages of *Ostertagia circumcincta* (Stadelmann) trichostrongylidae: I. Laboratory experiments. *Am J Vet Res* 1944;5:79-86.
13. Williams JC. Ecology and control of gastrointestinal nematodes of beef cattle. *Vet Clin North Am [Large Anim Pract]* 1983;5:183-205.
14. Williams JC, Knox JW, Baumann BA, et al. Seasonal changes of gastrointestinal nematode populations in yearling beef cattle in Louisiana with emphasis on prevalence of inhibition in *Ostertagia ostertagi*. *Int J Parasitol* 1983;13:133-143.
15. Michel JF. Arrested development of nematodes and some related phenomena. *Adv Parasitol* 1974;13:279-366.
16. Smeal MG, Donald AD. Effects on inhibition of development of the transfer of *Ostertagia ostertagi* between geographical regions of Australia. *Parasitology* 1981;82:398-399.
17. Michel JF, Lancaster MB, Hong C. Arrested development of *Ostertagia ostertagi* and *Cooperia oncophora*: effect of the time of the year on the conditioning and deconditioning of infective larvae. *J Comp Pathol* 1978;88:131-136.
18. Michel JF. Inhibition of development of *Trichostrongylus retortaeformis*. *Nature* 1952;169:933-934.
19. Eyszker M. Inhibition of the development of *Trichostrongylus* spp as third-stage larvae in sheep. *Vet Parasitol* 1978;4:29-33.
20. Hoberg EP, Zimmerman GL. Detection of ensheathed third-stage larvae of *Haemonchus contortus* in sheep: delayed exsheathment. *Proc Helminthol Soc Wash* 1987;54:150-153.
21. Kates KC, Turner JH. Observations on the life cycle of *Nematodirus spathiger*, a nematode parasitic in the intestine of sheep and other ruminants. *Am J Vet Res* 1955;16:105-115.
22. Boulenger CL. The life history of *Nematodirus filicollis* Rud, a nematode parasite of the sheep's intestine. *Parasitol* 1915;8:133-135.
23. Herlich H. The life history of *Nematodirus helvetianus* May, 1920, a nematode parasitic in cattle. *J Parasitol* 1954;40:60-70.
24. Thomas RJ. A comparative study of the life histories of *Nematodirus battus* and *N. filicollis*, nematode parasites of sheep. *Parasitology* 1959;49:374-386.
25. Beveridge I, Martin RR, Pullman AL. Development of the parasitic stages of *Nematodirus abnormalis* in experimentally infected sheep and associated pathology. *Proc Helminthol Soc Wash* 1985;52:119-131.
26. Levine ND. *Nematode parasites of domestic animals and of man*. 2nd ed. Minneapolis: Burgess Publishing Co, 1980.