A study was initiated to 1) determine which species of gastrointestinal nematodes are present in cattle in selected areas of Oregon, 2) examine the seasonal abundance of these nematodes as an indicator of periods of transmission and 3) determine at what season developmental inhibition occurs in the major genera of nematodes encountered. Four study sites representative of the major geographic regions within the state of Oregon were chosen: Corvallis, Langlois, near Fort Rock and southeast of Klamath Falls on the Oregon-California border. Eight sets of 3-4 tracer calves each were introduced onto pasture at each site over a 2 year period. Time of turnout onto pasture was dictated by the grazing season and corresponded to late spring, mid-summer, late fall and late winter.

At Corvallis, a distinct seasonality in parasite transmission (as indicated by nematode abundance) was evident with peaks occurring during the fall and winter. At Langlois, transmission was fairly constant throughout the year. However, no discernible patterns were evident at either Klamath Falls or Fort Rock.

A total of eight genera of nematodes were encountered during the study. Four (Ostertagia, Cooperia, Nematodirus and Trichostrongylus) were present at all study sites and were the most common genera at each. Trichuris was found at all sites except Klamath Falls. Oesophagostomum was present in tracers only from Langlois and Corvallis while Haemonchus was found only at Klamath Falls and Fort Rock. Capillaria was only present at Klamath Falls.
Where possible, specific transmission patterns for *Nematodirus*, *Cooperia*, and *Ostertagia* were determined for each site. *Nematodirus* was transmitted fairly steadily at both Langlois and Corvallis but was quite variable at Fort Rock. Developmental arrest was detected in this genus at all study sites during the fall and/or winter. *Cooperia* exhibited the most seasonally defined pattern of transmission with peak abundances during the fall and winter at Langlois, Corvallis and Klamath Falls. Hypobiotic larvae of *Cooperia* were present during the fall and/or winter only at Langlois and Corvallis. Peak transmission of *Ostertagia* at Langlois and Corvallis occurred during the fall and winter. At Fort Rock, transmission was lowest in the fall and increased in the winter. Hypobiotic larvae were evident in the fall and winter at Corvallis, Fort Rock and Klamath Falls. These data suggest Type II ostertagiasis may occur in late winter through spring in these areas. Hypobiotic larvae of *Ostertagia* were not detected at Langlois. The lack of appropriate environmental stimuli is one possible explanation for the apparent lack of hypobiosis at that site.
The Epizootiology of Gastrointestinal Nematodes of Cattle in Selected Areas of Oregon

by

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INTRODUCTION

Cattle of all ages, but particularly young and growing cattle, are affected by a wide variety of internal and external parasites. The internal parasites include the gastrointestinal nematodes, lungworms, liver flukes, adult and larval tapeworms and coccidia. External parasites include biting and non-biting flies, myiasis-producing flies, mosquitoes, lice, ticks and mites. According to Williams (1983), representatives of nearly all of these groups are found in cattle in all climatic and geographic regions. However, as disease-producing entities or as the causative agents in serious production and economic losses, the incidence of a particular group or groups is usually more restricted.

It is generally conceded that, of all the internal parasites, the gastrointestinal nematodes are of the most serious economic consequence. This is based on overall numbers of worms, numbers of genera and species present, general levels of pathogenicity and widespread distribution (see Williams, 1983). Under pasture conditions, it is the rule rather than the exception to encounter mixed infections of several genera of these nematodes. The most common genera present in North American cattle include Ostertagia, Trichostrongylus, Haemonchus, Cooperia, Nematodirus, Oesophagostomum and Trichuris (Williams, 1983; Gibbs and Herd, 1986). Of these, Ostertagia ostertagi is recognized as the most pathogenic and economically important parasite of cattle in temperate areas of the world. It can also cause severe problems in countries which have a sub-tropical climate provided there is also winter rainfall (Armour and Ogburne, 1982).

Work over the past 15-20 years has shown a marked variation in the transmission patterns of these nematodes depending on the particular geographic location in which they occur. It is, therefore, important that epizootiological data be developed for the various geographic areas as there are inherent problems in drawing generalized conclusions on the epizootiology of these parasites based on limited regional data. These
data do not exist for most of Oregon. Therefore, a study was initiated with three objectives: 1) To examine further the species composition of gastrointestinal nematodes of cattle in selected areas of Oregon; 2) To examine the seasonal abundance of these nematodes as an indicator of parasite transmission; 3) To determine when hypobiosis occurs in the major genera of nematodes encountered. Information obtained from this study should help fill the gaps in our knowledge on the epizootiology of gastrointestinal nematodes of cattle in Oregon.
REVIEW OF THE LITERATURE

As aspects of the epizootiology of the collective genera of the common gastrointestinal nematodes of cattle differ, each genus of nematodes will be discussed separately.

Genus: Trichostrongylus Looss, 1905

These are small (4-8 mm) worms parasitic in the alimentary tract of sheep, cattle and other vertebrates. Approximately 34 species have been described from mammals (Soulsby, 1982). Of these, Trichostrongylus axei (Cobbold, 1879), T. vitrinus Looss, 1905, T. colubriformis (Giles, 1892) and T. longispicularis Gordon, 1933 have been reported from cattle in the United States (Becklund, 1958; Becklund and Allen, 1958; Ciordia, 1975; Malczewski et al.; 1975; Craig, 1979; Williams et al., 1983; Baker et al., 1984).

Life Cycle

Most trichostrongylid nematodes have similar life cycles. Eggs are deposited on pasture in the feces of the host. The first-stage larvae (L₁) develop within the egg and hatch in one or more days. The larvae feed on bacteria, grow and molt in a day or more to the second-stage larvae (L₂). These larvae continue feeding and molt in a few days to the third-stage larvae (L₃). These L₃'s are the infective stage for the host. They are completely ensheathed within the cuticle of the L₂, whose oral and anal openings have been plugged. The L₃'s migrate out of the feces onto the vegetation. They do not feed, but live upon stored material. When ingested by an appropriate host, the larvae exsheath within the gastrointestinal tract. They grow and molt to the fourth-stage larvae (L₄) which, in turn, molt to adults. The length of time for adults to reach maturity and the length of the prepatent and patent period depends on the species of nematode, the species and age of the host and the host's previous exposure to the parasite.
Third-stage larvae of *Trichostrongylus* spp. develop from eggs held at constant temperatures between 6 and 32 C. The optimum temperature for development was found to be 25 C. At this temperature, L₃s develop within the egg and hatch within 3-7 days. Second-stage larvae can be found at 5-7 days with L₃s present at 7-9 days (Ciordia and Bizzell, 1963). Callinan (1978) found the mean developmental time to L₃s on herbage under ambient environmental conditions was 12.3 days.

After ingestion by the host, the L₃ exsheaths and can be found in the abomasum or small intestine 2-5 days later. The L₃ molts to the L₄ by day 7 and these, in turn, molt to adults by day 15. The prepatent period is around 21 days and patency may last up to 15 months (Ross et al., 1967; Levine, 1980).

Epizootiology

The development and survival of the free-living stages of *Trichostrongylus* spp., as with other nematodes, is dependant on weather and pasture conditions. In Great Britain, the most rapid development occurs in the summer with numbers of larvae on pasture peaking in 6-8 weeks. The infective larvae do have a limited ability to overwinter and, consequently, can infect young animals the following spring. However, larvae are unable to survive high temperatures and low humidities. Therefore, overwintered L₃s tend to die out at the beginning of summer (see Soulsby, 1982).

In Louisiana, Williams and Mayhew (1967) contaminated pasture plots every month for four years with feces containing eggs of three nematode species including *T. axei*. They found that larvae of this species survived up to 7 months when the plots were contaminated in the fall and early winter months. Larvae survived only up to 5 months when contaminated from February through May. The shortest survival (up to 4 months; usually only 1-3 months) occurred on plots contaminated in the summer. Decreasing larval survival times was found to be associated with high temperatures and extreme fluctuations in rainfall.
The pattern of transmission of *Trichostrongylus* spp. in the United States tends to depend on the region of the country. Although *T. axei* is continuously present in low numbers in animals from Texas and Louisiana, the main period of transmission is late winter through early spring (Craig, 1979; Williams et al., 1983, 1987). However, in California, the peak transmission period of this parasite occurs from late summer through fall (Baker et al., 1981).

While *T. colubriformis* and *T. vitrinus* arrest at the parasitic L₃ stage in sheep (see Gibbs, 1986), records of arrested development of *Trichostrongylus* spp. in cattle are few (Fitzsimmons, 1969). However, Baker et al. (1984) described a winter-spring pattern of hypobiosis for *T. axei* in California.

**Genus: Haemonchus** Cobb, 1898

Members of this genus are important pathogens in the abomasum of ruminants. There are between 9 and 11 valid species (Levine, 1980; Soulsby, 1982). Of these, only two are common in livestock in the United States. These are *Haemonchus contortus* (Rudolphi, 1803) which was described from sheep and *H. placei* (Place, 1893) which was described from cattle. *Haemonchus similis* Travassos, 1914, commonly found in deer in the southeast, has also been reported in cattle in the same area (Levine, 1980). Both *H. contortus* and *H. placei* develop in cattle and sheep and are morphologically similar; consequently, Gibbons (1979) synonymized the two species. However, Lichtenfels et al. (1986), after detailed studies of the synlophe, concluded that they are distinct species with *H. placei* predominating in most populations from cattle in the United States. This species is generally distributed throughout the United States (Becklund and Allen, 1958; Craig, 1979; Baker et al., 1981; Williams et al., 1983); however, it is somewhat sporadic in its occurrence in the more northern areas (Gibbs and Herd, 1986).
Life cycle

The life cycle of *H. placei* follows the typical trichostrongylid pattern. Eggs are shed in the feces with infective L₂s present in 1-3 weeks, depending on the time of year (Durie, 1961). Following ingestion of infective larvae, exsheathment occurs in the rumen. The parasitic L₂s then localize in the abomasum within 36 hours and penetrate between the epithelial cells, some as far as the muscularis mucosae. There, they molt to the fourth-stage between 36 and 76 hours after ingestion. The L₄s emerge from the gastric wall and molt to the adult stage 11-14 days after infection. The prepatent period is 26-28 days (Bremner, 1956). Patency generally lasts approximately 14 weeks with negative or low egg counts present after this time.

Arrested development in *H. placei* may occur at the L₄ and may last as long as 17 weeks. Two theories as to the cause of inhibition have been postulated, both based on the presence of mature or nearly mature nematodes in the abomasum. The first theory proposes that those larvae which develop faster produce a substance which has a direct inhibitory effect on the growth of slower developing larvae. The second theory says the host reacts to substances secreted by the more mature worms which causes the less developed worms to arrest (Bremner, 1956).

Epizootiology

Durie (1961) in Australia found that infective larvae of *H. placei* are present within and around the fecal pat in 1-3 weeks. As with other gastrointestinal nematodes of cattle, the fecal pat must remain soft or be broken by some mechanical means in order for the larvae to migrate away from the pat and be available to the host. *Haemonchus placei* larvae often migrate approximately 0.3 meters away from the fecal pat although distances of one meter may also be attained. Larvae survive well within fecal pats which may remain a source of contamination for up to 5 months when deposited in summer and 8 months when deposited in winter. However, larvae do not survive well after the fecal pat has
broken down and they are left without protection against the elements. Consequently, Gibbs (1979) found that, in Maine, carrier animals which contaminate the pastures with eggs are more important in the overwintering of Haemonchus spp. than are the larvae.

The seasonal transmission of Haemonchus spp. varies within the United States. In the Sacramento Valley of California, adults of H. placei are present in cattle from June through January with peak numbers occurring in late summer. Larval inhibition begins in late summer and continues through the winter (Baker et al., 1981). In Texas and Louisiana Haemonchus spp. can be recovered from cattle throughout the year; however, the peak transmission period is late spring, with larval inhibition occurring in the late summer and fall (Craig, 1979; Williams et al., 1983, 1987).

Genus: Cooperia Ransom, 1907

Species in this genus are parasitic nematodes found in the small intestine of ruminants. There are five species which commonly infect cattle in the United States. These are: C. punctata (von Linstow, 1907), C. pectinata (Ransom, 1907), C. oncophora (Railliet, 1898), C. surnabada Anitpin, 1931 and C. spatulata Baylis, 1938 (Soulsby, 1982; Gibbs and Herd, 1986). One other species, C. curticei (Railliet, 1893), which commonly occurs in sheep has occasionally been reported from cattle (Levine, 1980).

Le Roux (1936) reduced C. mcmasteri Gordon, 1932 to a junior synonym of C. surnabada. This action has been both supported and disputed. Allen and Becklund (1958) reviewed the available information regarding these two species and attempted to examine the types of both. Although unable to borrow specimens of C. surnabada from the Soviet Union, they did obtain specimens of C. mcmasteri from Australia. They concluded that the two species were probably identical; however, until specimens of C. surnabada could be examined, they advised that it should be regarded as distinct species.
In addition to this question, Isenstein (1971) found that when *C. surnabada* males were mated with populations of females containing a mixture of *C. surnabada* and *C. oncophora*, the progeny were comprised of a mixture of the latter two species. He interpreted this as evidence that *C. oncophora* and *C. surnabada* were polymorphs of the same species. However, recent workers in the systematics of this group of nematodes have studied structural attributes of North American species of *Cooperia* and have devised keys in which *C. mcmasteri* is identical to *C. surnabada* and *C. oncophora* is considered a valid species (Stringfellow, 1970; Lichtenfels, 1977).

**Life Cycle**

The life cycles of *Cooperia* species are similar to that of *Trichostrongylus* species. Under laboratory conditions, 25°C was found to be the optimum temperature for development of *C. punctata* and *C. oncophora* with *L₅s* present within 7-9 days. Development could also occur at lower temperatures (6-20°C) but the time required to reach the *L₅* increased as temperatures decreased (41 days at 6°C). Below 6°C and above 32°C, infective larvae of these two species did not develop (Ciordia and Bizzell, 1963).

The parasitic portion of the life cycles of *C. oncophora*, *C. pectinata* and *C. punctata* have all been studied and were found to be essentially the same (Stewart, 1954; Isenstein, 1963; Herlich, 1965a; Keith, 1967). Infective larvae exsheath within the rumen and pass to the anterior portion of the small intestine within 13 hours of ingestion. There is no histotropic stage; however, larvae do wrap around the villi of the small intestine, remaining in close contact with the mucosal surface throughout development. The parasitic *L₅s* molt to *L₆s* in 2-4 days and these become adults in 6-10 days. The prepatent period is 11-22 days (depending on the species present) and patency may last approximately 15 weeks for *C. pectinata* and up to 9 months for *C. punctata*. In his studies on the latter species, Mayhew (1962) found a
wide range in the patent period, extending from 4.5 to 63.5 months (x = 26.4 months).

Arrested development of *C. oncophora* has been shown to occur at the early fourth-stage (E4) (Michel et al., 1970a; Brunsdon, 1972; Smith, 1974). The evidence suggests that arrested development is caused by seasonal factors. Smith (1974) in the Maritime area of Canada, noted that inhibition of *C. oncophora* in calves grazing on pasture began to occur in late September when minimal daily temperatures approached 5 C and daylight hours were decreasing. Development of age resistance in the calves as a factor influencing larval inhibition was discounted because similar aged animals were used during both the early and late fall grazing periods; yet, only the those animals grazing in the late fall harbored inhibited larvae. Later work supported the theory that the environment (particularly cold temperatures) influences the developmental arrest of larval *C. oncophora*. Michel et al. (1974; 1975; 1978) and Smith (1978) showed that larvae stored at low temperatures (4 and 15 C) for up to 90 days or exposed to fall temperatures in the field exhibited an increased propensity for arrested development over larvae held above 17 C either in the laboratory or exposed in the field. Photoperiod had little or no effect on the induction of inhibition. Consequently, the evidence indicated that it was the environmental stimulus acting on the infective larvae and not seasonal changes in the host which was the primary influence triggering arrested development.

Epizootiology

The plowing and reseeding of pastures is thought to reduce the risk of infection with parasites by making the larvae unavailable for ingestion and preventing the eggs from hatching. However, Persson (1974) showed that eggs of *C. oncophora* survived 2-8 months when mixed with either peat moss, clay soil or sandy soil low in organic matter when held at 3 C. Under these same conditions, infective larvae were still alive after 1 year.
In order to assess whether eggs of *C. oncophora* would develop and hatch and infective larvae migrate to the surface and onto the vegetation after plowing into different types of soil at various depths, Persson (1974) buried feces containing either eggs or infective larvae in cylinders filled with one of the three soil types listed above. The cylinders were set in the ground such that the feces were at a depth of 10 or 20 cm below the surface. Cylinders were placed in the ground either in October or May and seeded with a mixture of oats, clover and grasses in May. Most eggs in manure buried in the three soil types during October were destroyed during the winter. Some eggs did hatch the following spring and infective larvae were found in the surface layer of the soil and on the herbage. There was no difference in larval counts between the two depths. Infective larvae in manure buried at 10 cm migrated to the surface and were recovered after only 10 days in all soil types as well as in the clay soil at 20 cm. Infective larvae survived the winter in greater numbers than the eggs and were recovered from the herbage during the following summer.

When egg-containing feces were buried in May, larvae were recovered in 16-27 days. The herbage larval count decreased over the summer followed by an increase in the fall. The following spring, larvae could still be recovered in herbage from the clay soil and peat moss with higher numbers of larvae recovered from cylinders with eggs at a depth of 10 cm. Infective larvae buried in May migrated to the surface in 16-27 days. The herbage larval count was high in the summer and decreased during fall. More larvae were recovered from 10 cm samples than from 20 cm samples and from moss or clay soil than from sandy soil. Only a small number of larvae were recovered the following spring. Persson (1974) concluded that plowing and harrowing fields contaminated with eggs and infective larvae of *C. oncophora* may reduce the number of infective larvae to some degree. However, a considerable number may survive, especially if the field is worked in the spring.

Goldberg and Lucker (1959) in Maryland demonstrated that infective *Cooperia* larvae could develop and be available for ingestion 3 weeks after the eggs had been deposited on pasture when deposition occurred in
the spring. Without recontamination, a reduction in the numbers of infective larvae occurred over the following 9 weeks. The numbers then remained relatively constant during the fall with some larvae surviving over the winter. Survival of Cooperia spp. larvae during harsh winter conditions has also been noted to occur in Wyoming (Schwink, 1963), Maine (Gibbs, 1980) and the Maritimes in Canada (Smith, 1972).

Williams and Mayhew (1967) studied the survival of C. punctata larvae under Louisiana conditions. Pastures were contaminated once a month for four years with cattle feces containing nematode eggs. They found that larvae survived longest (up to 8 months) on plots contaminated in the fall and early winter months (September through January). On those plots contaminated from February through May, larvae survived up to 5 months while larvae on those plots contaminated during the summer (June through August) survived the shortest amount of time (up to 4 months). This decrease in survival time was attributed to continued high temperatures and extreme fluctuations in the amount and occurrence of rainfall.

The transmission patterns of the species of Cooperia in the North America also varies with the region. In Louisiana and Texas, transmission may begin around April and last for 9-12 months. Peak transmission occurs during the winter or spring with larval inhibition occurring in late winter (Craig, 1979; Williams et al., 1983, 1987). In California, transmission occurs year round. However, the timing of arrested development varies with this phenomenon peaking in the winter in the Sacramento Valley while little or no inhibition occurs in northern California (Baker and Fisk, 1986; Baker et al., 1981, 1984; Padilha-Charles, 1985). In Maine, transmission occurs year round peaking in the fall and winter. Developmental arrest begins occurs during the winter (Randall and Gibbs, 1977). In the Maritimes of Canada C. oncophora begins to undergo arrested development in the fall (Smith, 1974). In western Oregon where the grazing season lasts from May through October, Syhre et al. (1987) indicated that peak transmission of C. oncophora occurred in the fall. No inhibited development of this species was noted.
Genus: **Ostertagia** Ransom, 1907

Several species within this genus occur in cattle throughout North America. **Ostertagia ostertagi** (Stiles, 1892) is the most common species found in cattle and, along with **O. lyrata** Sjoberg, 1926, is generally distributed across the United States (Gibbs and Herd, 1986). **Ostertagia bisonis** Chapin, 1925 has also been reported to occur in cattle in the western United States (see Becklund and Walker, 1967). A fourth species, **O. kolchida** Popova, 1937 was only recently reported for the first time from cattle in North America (Rickard and Zimmerman, 1986).

In Britain, Hong et al. (1981) noted that **O. lyrata** only occurred when **O. ostertagi** was present and then only in low numbers. They noted the same was true for **O. kolchida** and **O. leptospicularis** Asadov, 1953 with **O. kolchida** being the minor species. Consequently, they felt that each pair of nematodes did not behave as two separate competing species, but rather as two morphs of a single polymorphic species. Subsequent breeding experiments and further morphological data substantiated this viewpoint (Lancaster et al., 1983; Lichtenfels et al., 1988). Consequently, the suggestion has been made to place the minor species of each species pair in synonymy with the respective major species.

**Life Cycle**

The life cycle of **O. ostertagi** has been reviewed in detail by Threlkeld (1946, 1958), Douvres (1956) and Rose (1969). It is direct and essentially similar to those of other members of the Trichostrongylidae. The eggs are passed in the feces and the L₁ hatches in 12-24 hours. The L₁ begins to molt to the L₂ on the third day followed by the molt to the L₃ around the fifth to sixth day. Ciordia and Bizzell (1963) found the optimum temperature for development to be 25 C. Lower temperatures (6-20 C) prolonged the rate of development while little or no larval development occurred at 5 C or above 35 C. These results were later confirmed by Pandey (1972a). Pandey (1972b)
found that eggs, L₁s and L₂s were killed by high temperatures (40-50 °C) but survived fairly well (50 weeks +) at lower temperatures (4 °C).

Development to the infective stage usually occurs within the fecal pat and the L₂ then migrates under moist conditions onto the herbage. Infection of the host is through ingestion of the L₂. Exsheathment occurs in the rumen and the L₂ then penetrates the gastric glands in the abomasal mucosa. The L₂ molts to the L₃ in 3-8 days and adults are present as early as 12 days after infection. The prepatent period is 17-21 days. Peak egg output usually occurs approximately 25 days after infection and then declines logarithmically (Michel, 1969a).

The timing of development of the parasitic stages of O. leptospicularis is essentially the same as for O. ostertagi with the third molt occurring 3-5 days after infection and adults present as early as day 10 (Bisset et al., 1984).

Arrested development in the genus Ostertagia occurs in the E₁. Although to date the phenomenon of larval arrest has been most extensively studied in infections of O. ostertagi in cattle, it was not considered important until Martin et al. (1957) suggested an outbreak of parasitic gastritis in housed cattle was due to the maturation of worms which had been arrested at the E₁. Subsequent work has suggested that there are three factors influencing larval inhibition of Ostertagia. The first factor is the immune state of the host. Michel (1963) observed that the number of E₁s increased in calves which received constant numbers of infective larvae daily. Furthermore, in two calves which failed to develop resistance, the number of E₁s was much smaller than in responsive calves killed at a corresponding stage of the experiment. Therefore, it was concluded that inhibited development was an expression of host resistance. Ross (1963) also saw evidence which supported this view in experiments which showed a larger proportion of a second infection underwent arrest than of the initial infection. However, later Ross and Dow (1964) were unable to confirm these results and work by Michel (1969b) and Michel et al. (1973a) also did not support this hypothesis. More recent work, though, has suggested host resistance factors do play a part in induction of immune-mediated arrest
The second factor, which has come to be accepted as the primary stimulus of larval inhibition, stemmed from observations by Anderson et al. (1965a,b) that large numbers of inhibited *Ostertagia* were present in helminth-naive tracer calves which had grazed in the autumn. Subsequently, numerous experiments were conducted in which larvae were "conditioned" by subjecting them to stimuli which simulated autumn in the laboratory, by exposing them to actual autumn conditions in the field or by simply storing the larvae at 4°C. Results indicated that conditioning did induce arrest (see Michel, 1974; Armour and Ogburne, 1982). Consequently, it became accepted that environmental factors are the major influence in the induction of arrest. However, the mechanisms by which they affect larvae are still unknown. It has been suggested by several authors that two distinct strains of *O. ostertagi* exist, one having the propensity to arrest and the other being "normal" (Armour et al., 1967a,b; Michel 1967a,b; Sollod, 1967). However, research into this third factor received little attention until Michel et al. (1973b) demonstrated a greater propensity for developmental arrest in the progeny of worms whose own development had been arrested. Then, Smeal et al. (1980a,b) reported that isolates of *O. ostertagi* from different areas of Australia displayed a varying tendency to arrest. Smeal and Donald (1981) transferred two of the isolates, each with a different propensity to arrest and from different climatic regions, to their opposite environments. The worms arrested to the same degree in the opposite region as in the region from which they originally came suggesting that the propensity to arrest may be a genetically controlled, heritable trait. Frank et al. (1986, 1988) in a similar experiment conducted in the United States obtained similar results also indicating the pattern of hypobiosis of *O. ostertagi* in beef cattle is genetically determined.
Epizootiology

Both the eggs and L₃s of *O. ostertagi* survive well over the winter on pasture (Goldberg and Rubin, 1956; Bell et al., 1960; Rose 1961, 1970; Schwink, 1963) or when buried in the ground (Persson, 1974). However, very few will survive a second winter (Smith, 1972; Gibbs, 1980). Numbers of infective larvae also decrease over the summer (Smith and Archibald, 1969; Smith, 1972; Gibbs, 1980). Consequently, Gibbs (1979) concluded that larval survival on pasture over the first winter was of greater importance than carrier animals as sources of infection of *O. ostertagi* for young, susceptible calves.

The vast majority of work concerning the epizootiology of bovine ostertagiasis has been conducted in Britain. Michel (1969c) and Michel et al. (1970b) demonstrated that the number of L₃s on pasture followed a distinct seasonal pattern with only one or two generations produced each year. Larvae on herbage was found to be low in April and declined very rapidly through June. Numbers then increased dramatically in July and August with a progressive decline through autumn and winter, reaching fairly low levels again in April. To maintain this cycle, these authors demonstrated that eggs deposited on pasture in April, May and June first appear as L₃s on herbage in July or August. In August and September, developmental time begins to increase in length and little or no development takes place after September. Inhibition-prone larvae are acquired by cattle in late autumn remaining inhibited in the host during winter.

Until recently, our understanding of *O. ostertagi* in this country was based on information compiled in the United Kingdom as it was assumed that the transmission patterns and timing of disease would be similar to Scotland and England. At first, this appeared to be the case. In 1972, larval inhibition during late autumn and the subsequent winter-spring type of disease was observed in Canada (Smith and Perrault, 1972). Randall and Gibbs (1977) then demonstrated the transmission of this nematode in Maine was high in March-April and again in September-December with arrested development occurring in November-
February. Larval inhibition during winter has also been documented in Washington (Malczewski et al., 1975), the northern coast of Oregon (Kistner et al., 1979), Idaho, Maine (Gibbs, 1979), Michigan (Schillhorn van Veen and Melancon, 1984), Ohio (Herd, 1980) and implicated indirectly in Kentucky (Lyons et al., 1981). However, this pattern broke down in the southern temperate regions of the U.S. In contrast to the northern areas, larval development was shown to occur during the winter resulting in large numbers of L3s available from November-May, with peaks in January and February (Williams and Bilkovitch, 1971, 1973; Craig, 1979). Consequently, transmission may occur year-round as in Louisiana or from early winter through spring as in Texas. Peak transmission occurs from late winter to early spring with larval inhibition beginning to occur in the spring (Craig, 1979; Williams et al., 1983, 1987). Therefore, disease due to the normal development of adult *Ostertagia* (Type I) is likely to be a winter problem and disease due to the maturation of inhibited larvae (Type II) is likely to be a summer-autumn problem, the reverse of the pattern seen in the northern U.S. Spring inhibition of larvae has also been found to occur in Georgia (Ciordia et al., 1971), Missouri (Brauer, 1983), Florida (Courtney et al., 1986) and indicated indirectly in Oklahoma (Schillhorn van Veen and Melancon, 1984).

The epizootiology of *O. ostertagi* in California represents a modified pattern of the two extremes. Baker et al. (1981) report that, on irrigated pastures in the Sacramento Valley, two very distinct peaks of transmission occurred. The first was in March and the second in November-December with low levels occurring the rest of the year. Arrested development occurred during the spring, an observation later confirmed by Padilha-Charles (1985). Consequently, Baker et al., (1981) suggested that Type I ostertagiasis could be expected in either the spring or fall while Type II ostertagiasis would be expected during the fall. In the high Sierra Mountains of northern California, Baker et al., (1984) found that *O. ostertagi* was also transmitted year-round but with maximum transmission only during late winter through spring. Inhibition occurred to some extent in the winter but reached peak values
in the spring. Finally, in the foothills of the Sierra Mountains Baker and Fisk (1986) again found year-round transmission of this parasite. However, in comparison to the other two areas of California studied, the peak transmission period was much extended (late fall-spring). Inhibition was also a spring phenomenon.

Genus: Nematodirus Ransom, 1907

Only one species within this genus, N. helvetianus May, 1920, is considered to be primarily a parasite of cattle in North America. Two others, N. filicollis (Rudolphi, 1802) and N. spathiger (Railliet, 1896) have been reported in cattle but are more often associated with sheep (Wright and Anderson, 1972; Soulsby, 1982).

Nematodirus helvetianus occurs in the small intestine of its host. It is widespread across North America being found in cattle from Canada (Frechette and Gibbs, 1971; Smith, 1974; McGregor and Kingscote, 1957) through the southern United States (Becklund and Allen, 1958; Ciordia et al., 1971), and from Maine (Randall and Gibbs, 1977) to Washington (Malczewski et al., 1975), Oregon (Kistner and Lindsey, 1974) and California (Baker et al., 1981).

Life Cycle

The life cycle of N. helvetianus differs somewhat from the typical trichostrongyloid pattern. The first two larval molts occur within the egg rather than the L; hatching and development proceeding external to the egg. Zviagintsev (1934) found development of Ls occurs within a wide range of temperatures (3-29 C) with the optimum temperature being 28 C. At 34-35 C, 50% of the eggs died while all died at 38-39 C. Herlich (1954) confirmed these observations and noted also that eggs held at cold temperatures (-10 C and 3 C) for short periods of time (1-3 weeks) would develop when placed at 28 C.

Herlich (1954) noted that the first-stage larvae were present within the egg after 64 hours of incubation at 28 C. By 96 hours, Ls
were present within the egg. Hatching began on day 8 of incubation at this temperature and on day 17 when held at 22 C. After ingestion by cattle, L₃s exsheath within the small intestine and develop to L₄s within 8 days. The larvae do not penetrate the intestinal wall, but remain in close contact with the villi. The adult stage is reached approximately 15 days after ingestion of the L₃. The prepatent period is 21-26 days and the patent period is 12-132 days in calves 1-10 months old.

Developmental arrest of *N. helvetianus* has been shown to occur at the E₄. As with species of *Cooperia*, environmental factors appear to be responsible for induction of arrest (Smith, 1974).

**Epizootiology**

Rose (1966) in southeast England examined the timing of development to the L₁ when eggs were placed on field plots at various times of the year. The shortest developmental times of 4-5 days occurred in May-August. The longest times were during the months of September and October when development took 33-34 days. Developmental times gradually decreased over the remaining months from 26-28 days in November to 7 days in April. The maximum survival period of eggs and hatched L₃s was approximately 2.5 years when eggs were placed on plots in September. The free L₃s survived best at low, non-freezing temperatures but could live as long as 32 weeks when frozen at -3 to -4 C. However, the L₃s were quite susceptible to desiccation. They were killed in 8 weeks at 70% relative humidity at 27 C.

In Canada, Smith (1972) demonstrated that *N. helvetianus* could survive over two winters and the intervening grazing season on marshland pastures under Maritime climatic conditions. Although it was not determined precisely when the larvae developed on pasture, he postulated that the continuous presence of L₃s may have been due to both the continual hatching of eggs and to the longevity of the larvae after hatching. In Maine, Gibbs (1979, 1980) also demonstrated that *N. helvetianus* could survive over a 2 year period and concluded that the
overwinter survival of this parasite on pasture is more important than carrier animals as sources of infection for susceptible calves grazing pastures the following spring.

The transmission of *N. helvetianus* may be seasonally defined as occurs in northern California (Baker and Fisk, 1986) or may occur nearly year-round as in Maine (Randall and Gibbs, 1977) and in other parts of California (Baker et al., 1981, 1984). Arrested development, when it does occur, usually takes place in late fall to winter (Smith, 1974; Randall and Gibbs, 1977; Baker et al., 1981).

Genus: *Oesophagostomum* Molin, 1861

Species within this genus are commonly called nodular worms due to the nodules which often form in the small intestine and sometimes the cecum and large intestine. This is in response to larval development which occurs within the intestinal wall. The adult worms live in the lumen of the cecum and large intestine. Only *O. radiatum* (Rudolphi, 1803) is commonly found in cattle in North America (see Levine, 1980) although it appears to be more prevalent in the southern United States (Gibbs and Herd, 1986). A second species, *O. venulosum* (Rudolphi, 1809) has occasionally been reported in cattle and may supplement or replace *O. radiatum* in cattle in some parts of the western United States (Baker and Fisk, 1986; Hoberg et al., 1988). The nodular worm of sheep, *O. columbianum* (Curtice, 1890), will not mature in calves, but only develops to the L₄ (Herlich, 1970).

Life Cycle

Andrews and Maldonado (1941), Anantaraman (1942) and Roberts et al. (1962) described the life cycle of *O. radiatum*. Eggs are passed in the feces. The optimum temperature for larval development is 24-32 C. The L₁ develops and hatches from the egg within 12-20 hours. The first molt occurs approximately 24 hours after hatching. The L₂ then molts to the L₃, beginning 86-90 hours after hatching from the egg. The L₃ is
apparently quite short lived, lasting only 2-3 months when stored in water at room temperature.

Infection of the host occurs upon ingestion of the L₃, although Mayhew (1939) and Gerber (1975) have demonstrated that infections may become established through larval penetration of the skin. The larvae exsheath and, subsequently, penetrate the small intestine and sometimes the cecum or large intestine. The parasitic L₃ grows rapidly and molts to the L₄ between 4 and 10 days after ingestion. The L₄ then returns to the lumen of the gut beginning 7-14 days after ingestion. Larvae pass to the cecum or colon and molt to the adult stage between days 17 and 29. The prepatent period ranges between 26 and 41 days, but is usually around 37 days. Egg production peaks during weeks 6-10 of infection and usually remains high for 1-4 weeks. It then declines rapidly and most adults are eliminated, although Mayhew (1950, 1962) has shown some worms can live in calves and produce eggs for 11-15 months. Inhibited development for any species of Oesophagostomum has not clearly been demonstrated.

Epizootiology

Although O. radiatum appears to be generally distributed throughout North America (Gibbs and Herd, 1986) little is known about the transmission patterns of this parasite. Goldberg and Lucker (1959) in Maryland found a calf became infected by grazing a pasture in the spring 21 days after having been contaminated with eggs. Few worms were recovered from calves grazed on the pasture 63 days after contamination and none 171 days after contamination.

Williams and Mayhew (1967) studied the survival of O. radiatum larvae on pasture in Louisiana. Although larval survival varied from year to year, the longest survival times (up to 6 months) were noted to occur in plots contaminated with eggs in the fall and early winter months. Larvae survived up to 4 months on plots contaminated in February through March. The shortest survival time was on plots contaminated through the summer. Although some larvae lived up to 4
months, survival usually extended for only 1-3 months. They concluded
that optimal conditions for larval development and survival on pasture
were mean monthly mean temperatures of 13-26 C plus total monthly
precipitation of 5-12 cm. Optimum conditions for larval survival alone
occurred when mean monthly mean temperatures were 8-26 C and total
monthly precipitation was 5-17 cm.

Baker and Fisk (1986) saw that transmission of O. venulosum in
northern California was too sporadic to draw any definite conclusions.
However, their data indicated the possibility of a hypobiotic phase
occurring during the summer.

Genus: Trichuris Roederer, 1761

Nematodes in this genus are commonly referred to as whipworms as
they resemble a buggy whip. All whipworms live in the cecum of their
host where they attach to the mucosa by burying the anterior end into
the tissue. Only 7 species of Trichuris are known to occur in North
America (Knight, 1974, 1983; Rickard, unpublished data). Of these only
two, T. ovis (Abildgaard, 1795) and T. discolor (von Linstow, 1906),
occur in cattle (Knight, 1971; Levine, 1980). Details on the life cycle
and patterns of transmission for the bovine whipworms have apparently
not been examined in North America. Likewise, little is known about the
pathogenesis of infection. Ordinarily, they are present in small
numbers which produce no detectable effects. However, Smith and
Stevenson (1970) in Canada and Georgi et al. (1972) in New York did
describe fatalities due to T. discolor infections in calves. Clinical
signs included heavy diarrhea and progressive emaciation. Heavy
Trichuris infections with hemorrhagic inflammation of the colonic mucosa
was found on necropsy.
MATERIALS AND METHODS

Study Sites

Four study sites were chosen based on geographic and climatic regions within the state. Site A is the Oregon State University (OSU) Beef Ranch located about 20 km northwest of Corvallis. This site has a moderate climate. Although summers are hot and dry, the remainder of the year is relatively mild with high amounts of rainfall especially during the winter (Figure 1). The ranch maintains a cow-calf operation (about 150 cows) with both spring and fall calving. As this is an experimental unit, introductions of new animals on pasture occurs frequently. The grazing season begins approximately April 1 and lasts until mid-September. Supplemental feeding with baled hay is started in July and continues through the winter.

Site B is located at Langlois on the southern Oregon coast. While temperatures fluctuate relatively little, precipitation varies in the same manner as site A being high late fall through spring and low over the summer (Figure 2). The primary cattle ranch is a cow-calf operation (300 cows) on 875 acres. Calves born in the spring are sold that fall. At this time, replacement heifers are moved to a second ranch of 1150 acres where they are raised and brought through their first calving. They then return to the primary ranch the fall following their first calving as coming 3-year-olds. The second ranch also supports about 900 ewes. The cattle are treated with anthelmintics in the spring after calving and again in the fall at weaning time. Younger animals may be treated more frequently. Pastures are not irrigated and consist of New Zealand white clover, ryegrass and orchard grass. The grazing season extends from mid-April through November. Supplemental feeding with grass hay begins late November or December and continues through mid-April.

Site C is split into two locations: the border ranch is approximately 59 km southeast of Klamath Falls on the California-Oregon border and the home ranch is located about 15 km west of Klamath Falls. The summers are hot and the winters harsh with low amounts of
Figure 1. Mean monthly maximum and minimum air temperature (top) and total monthly precipitation (bottom) for Corvallis, Oregon (29 year average).
Figure 2. Mean monthly maximum and minimum air temperature (top) and total monthly precipitation (bottom) for Bandon, Oregon (29 year average).
precipitation occurring the year round (Figure 3) This is an 1100 head cow-calf operation on 1800 acres. Calving occurs mostly in the spring; however, some fall calving also takes place. Pastures consist of irrigated grasses with flood irrigation occurring between late spring and late fall. Cows are turned out on the border ranch in April where they graze until November when they are returned with their calves to the home ranch. Supplemental feeding of alfalfa hay occurs only at the home ranch during December through April. Cattle are routinely treated with anthelmintics prior to leaving the home ranch and again upon their return. With the exception of the last group, tracer calves were grazed only at the border ranch.

Site D is located approximately 24 km southwest of Fort Rock in central Oregon. As this is in the high desert region, precipitation is quite low year-round with harsh winters and hot summers (Figure 4). This ranch runs 115 cows, 120 feeders and 120 sheep on 1345 acres. Calving is spread out from October through April. Much of the ranch consists of irrigated pasture grasses or alfalfa. Sprinkler irrigation occurs between May and mid-September. The grazing season is short compared to the previous sites, beginning in May and lasting until September. Alfalfa aftermath allows an additional one or two months of grazing prior to supplemental feeding of alfalfa hay. Supplemental feeding continues through April. The sheep are rotated through the pastures following the cattle. Only new animals brought in are treated with anthelmintics.

All climate data was provided by the OSU Climatic Research Institute and were recorded at the following locations: Hyslop Field about 12.5 km from site A; Bandon, about 23 km north of site B; Round Grove about 45 km northeast of site C; Silver Lake Ranger Station about 30 km southwest of site D.

Tracers

Tracer calves were Holstein bull calves 5 months of age or younger. These animals had been raised in confinement since birth at the OSU
Figure 3. Mean monthly maximum and minimum air temperature (top) and total monthly precipitation (bottom) for Round Grove, Oregon (29 year average).
Figure 4. Mean monthly maximum and minimum air temperature (top) and total monthly precipitation (bottom) for Silver Lake Ranger Station (17 year average).
Dairy Barn. Calves were transported to the various ranches and turned out onto pasture within 4 days of arriving at the ranch. Placement of tracer calves at each location was dependent upon the climatic conditions as reflected by the grazing season. A minimum of three tracers are placed on pasture near the beginning (spring), middle (mid-summer) and end (late fall) of the grazing season and at least once during the winter. Tracer calves were grazed along side the resident cattle population. Tracers grazing at the Langlois site were vaccinated against Clostridia spp., parainfluenza-3 and infectious bovine rhinotracheitis prior to turnout.

After grazing, tracers were returned to either the Veterinary Medicine Animal Isolation Unit or the OSU Beef Barn to be held in isolation for a minimum of two weeks to allow for maturation of worms. They were then killed and necropsied for parasite recovery.

In the event calves were not available from Dairy Science, replacement animals were purchased at auction. These animals were 4-6 months in age when purchased and consisted of various beef breeds. These calves were treated twice with fenbendazole at 5 mg/kg and held in isolation until assigned to a study site. Fecal examinations were performed to evaluate parasite burdens on the day of purchase, at each anthelmintic treatment and 2 weeks after the final treatment. No calf was passing nematode eggs after the first anthelmintic treatment. It was only necessary to use replacements at the Klamath Falls (4 times) and Fort Rock (3 times) study sites.

Necropsy Techniques

Necropsy procedures were modified from those recommended by the Food and Drug Administration (1981) and the World Association for the Advancement of Veterinary Parasitology (1981). At necropsy, the abomasum, small intestine and cecum with first meter of the colon were ligated in situ, removed from each animal and separated. Each organ was opened longitudinally into separate containers and the contents collected. The mucosal surface was rubbed vigorously (referred to as
stripping) and the washings added to the contents. The contents of the abomasum were then brought to a known volume from which two separate 5% aliquots were saved. These were washed with tap water through a 400-mesh (37.5 μm opening) sieve. The material retained on the screen was backwashed into a dish and preserved in 10% neutral buffered formalin. The small intestinal contents were handled in the same manner. The entire contents of the cecum-colon were washed through a 100-mesh (150 μm opening) sieve and the material retained placed in jars and preserved as above. The abomasum was further processed by placing it in tap water in a covered container and either incubating 4-6 hours at 37.5 C or allowing to stand at room temperature for approximately 16-20 hours. The incubating fluid was saved and the abomasum again stripped by hand and the washings added to the fluid. Samples from the abomasal incubate were handled as for the abomasal contents with the exception that two 50% aliquots were saved. The parasites were subsequently removed from one of the two samples obtained from each organ, identified and enumerated. Total counts were then calculated by multiplying the number of each species recovered in a sample by the dilution of that sample. In cases where the nematodes were too numerous to count, subsamples were taken and total numbers calculated accordingly.
RESULTS

In all, a total of nine tracer calves died during the minimum 14 day isolation period subsequent to grazing pastures: Corvallis - fall, 1985, two at 6 days, one at 7 days and one at 12 days; Langlois - fall, 1985, one at 1 day, one at 2 days; spring, 1986, one at 8 days; Klamath Falls - spring, 1985, one at 5 days; Fort Rock - fall, 1986, one at 13 days. All except the four at Corvallis in the fall of 1985 were considered to have died from causes not directly related to parasitism. The stress of transportation in inclement weather combined with pneumonia (as was evidenced at necropsy) were considered to have been the primary factors contributing to the mortality of these calves.

Site A - Corvallis

The mean monthly minimum and maximum air temperature did not deviate considerably from the 29 year average except for December, 1985 when the minimum temperature was 5 C below normal. Overall, the precipitation also did not deviate considerably except for the months of December, 1985 and 1986 when the precipitation was 10 and 11 cm below normal, respectively and February, September and November, 1986 when it was 5 cm or more above normal.

The total number of nematodes present in the tracer calves showed a distinct seasonality with high numbers present in the fall and winter and very low numbers in the spring and summer (Figure 5). There was a total of six genera of nematodes recovered from the tracers during the study (Table 1). Of these six, Ostertagia, Cooperia and Nematodirus predominated with Trichostrongylus, Trichuris and Oesophagostomum occasionally encountered. Cumulatively, Cooperia was the most abundant genus present closely followed by Ostertagia.

On a seasonal basis, the abundance of Nematodirus was low in the spring of both years examined (Figure 6). The abundance then increased through the summer or fall and declined somewhat in the winter. Early-fourth stage larvae were recovered during the fall, 1985 and winter and
Figure 5. Total number of nematodes recovered from tracer calves at the Corvallis study site.
Table 1. Species composition and abundance of nematodes recovered from tracer calves at the Corvallis study site.

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<th>F</th>
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<td>507</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>0</td>
<td>33</td>
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</tr>
<tr>
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<td>275</td>
<td>20</td>
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</tr>
<tr>
<td>T. leptospicularis</td>
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<td>225</td>
<td>0</td>
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<td>0</td>
<td>0</td>
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</tr>
<tr>
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<td>0</td>
<td>0</td>
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</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nematodirus spp.</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N. helvetianus L.</td>
<td>85</td>
<td>920</td>
<td>6450</td>
<td>2968</td>
<td>80</td>
<td>893</td>
<td>507</td>
<td>107</td>
</tr>
<tr>
<td>N. helvetianus E.</td>
<td>30</td>
<td>910</td>
<td>7700</td>
<td>2568</td>
<td>73</td>
<td>607</td>
<td>293</td>
<td>133</td>
</tr>
<tr>
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<td>180</td>
<td>3650</td>
<td>533</td>
<td>13</td>
<td>40</td>
<td>27</td>
<td>400</td>
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<tr>
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<td>0</td>
<td>4750</td>
<td>567</td>
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<td>0</td>
<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>Oesophagostomum venulosum</td>
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<td>0</td>
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</tr>
</tbody>
</table>

*Sp = spring; Su = summer; F = fall; W = winter.

1L = late-fourth stage larvae
2E = early-fourth stage larvae
Figure 6. Total number of *Nematodirus* spp. recovered from tracer calves at the Corvallis study site (top) and percent of total represented by early-fourth stage larvae (*E*₄), late-fourth stage larvae (*L*₄), and adults (bottom).
summer, 1986. However, proportions indicate only possible inhibition during the fall, 1985.

The abundance of Cooperia was distinctly seasonal with peaks occurring in the fall and winter of both years (Figure 7). Early-fourth stage larvae were recovered in substantial numbers also in the fall and winter in proportions indicating developmental inhibition.

The peak abundance of Ostertagia occurred in the winter with equivalent numbers sometimes present during the preceding fall (Figure 8). Early-fourth stage larvae were present during each spring, fall and winter; however, proportions indicate inhibition only for the fall and winter populations.

Site B - Langlois

The mean monthly minimum and maximum air temperatures did not deviate substantially from the 29 year average. However, total monthly precipitation did vary considerably. The precipitation during the first four months of 1985 was consistently well below normal (3-24 cm). June then showed an increase in precipitation of approximately 5 cm above average. The precipitation then remained about average until November and December when it dropped to 7 and 15 cm below normal, respectively. In 1986, the first eleven months were either approximately normal or well above the 29 year average. Only December was substantially below normal (17 cm). In 1987, January was 8 cm above normal, February and March were approximately normal and April was 8 cm below the average.

For the total number of nematodes present at this site, a pattern of low numbers in the summer followed by increases in the fall and winter was exhibited (Figure 9). The same six genera of nematodes encountered at Corvallis were also present at Langlois (Table 2). Ostertagia, Cooperia and Nematodirus were again the most prevalent. On a cumulative basis, Nematodirus was the most abundant nematode genus at Langlois closely followed by Ostertagia.

Seasonally, the abundance of Nematodirus was fairly constant (Figure 10). Early-fourth stage larvae were recovered consistently in
Figure 7. Total number of *Cooperia* spp. recovered from tracer calves at the Corvallis study site (top) and percent of total represented by early-fourth stage larvae (E₄), late-fourth stage larvae (L₄) and adults (bottom).
Figure 8. Total number of Ostertagia spp. recovered from tracer calves at the Corvallis study site (top) and percent of total represented by early-fourth stage larvae ($E_4$), late-fourth stage larvae ($L_4$) and adults (bottom).
Figure 9. Total number of nematodes recovered from tracer calves at the Langlois study site.
Table 2. Species composition and abundance of nematodes recovered from tracer calves at the Langlois study site.

<table>
<thead>
<tr>
<th>Parasite</th>
<th>Sp '85</th>
<th>Su</th>
<th>F</th>
<th>W '86</th>
<th>Sp</th>
<th>Su</th>
<th>F</th>
<th>W '87</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ostertagia spp.</td>
<td>4951</td>
<td>308</td>
<td>150</td>
<td>2719</td>
<td>791</td>
<td>83</td>
<td>6520</td>
<td>3780</td>
</tr>
<tr>
<td><em>O. ostertagia</em></td>
<td>4204</td>
<td>271</td>
<td>876</td>
<td>1955</td>
<td>428</td>
<td>41</td>
<td>6293</td>
<td>3434</td>
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<tr>
<td><em>O. lyrata</em></td>
<td>19</td>
<td>2</td>
<td>4</td>
<td>23</td>
<td>1</td>
<td>0</td>
<td>133</td>
<td>33</td>
</tr>
<tr>
<td>Teladorsagia circumcincta</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td><em>O. ostertagia</em></td>
<td>133</td>
<td>7</td>
<td>295</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>253</td>
<td>33</td>
</tr>
<tr>
<td>Ostertagia E.</td>
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<td>4</td>
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<td>0</td>
<td>47</td>
<td>27</td>
</tr>
<tr>
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<td>222</td>
<td>220</td>
<td>13</td>
<td>2667</td>
<td>1133</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>C. burnabada</em></td>
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<td>0</td>
<td>0</td>
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</tr>
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<td>0</td>
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<td>0</td>
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<tr>
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<td>0</td>
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<tr>
<td><em>T. circumcincta</em></td>
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<td>47</td>
<td>7</td>
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<td>7</td>
<td>4640</td>
<td>7</td>
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<td><em>I. axei</em></td>
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<td>0</td>
<td>20</td>
<td>0</td>
<td>2207</td>
<td>7</td>
</tr>
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<td><em>I. vitrinus</em></td>
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<td>0</td>
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<td>0</td>
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<td><em>I. losinipinellis</em></td>
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<td>0</td>
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<td>0</td>
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<td>0</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
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</tr>
<tr>
<td><em>Nematodirus spp.</em></td>
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<td>1933</td>
<td>647</td>
<td>1467</td>
<td>73</td>
<td>17574</td>
<td>2322</td>
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<td>1013</td>
<td>1493</td>
<td>533</td>
<td>1193</td>
<td>283</td>
<td>21707</td>
<td>827</td>
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</tr>
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<td>13</td>
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<td>47</td>
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<td>80</td>
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<td>1</td>
</tr>
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<td>12</td>
<td>0</td>
</tr>
</tbody>
</table>

1Sp = spring; Su = summer; F = fall; W = winter.
2E = early-fourth stage larvae.
3L = late-fourth stage larvae.
Figure 10. Total number of *Nematodirus* spp. recovered from tracer calves at the Langlois study site (top) and percent of total represented by early-fourth stage larvae ($E_4$), late-fourth stage larvae ($L_4$) and adults (bottom).
the fall and/or winter of each year in proportions which indicate inhibition. In contrast, *Cooperia* was virtually absent during the summer (Figure 11). Increases in abundance were noted each of the subsequent falls with numbers remaining elevated over the winter into the spring. Early-fourth stage larvae were recovered only during the fall of each year with the proportions indicating inhibition occurred only during the fall of 1986.

As with *Cooperia*, the total number of *Ostertagia* was lowest during the summer (Figure 12). The abundance then increased each fall with transmission occurring over the winter and into the spring. Substantial numbers of E₄s were recovered only once, during the fall of 1985. However, the proportion was approximately equal to the L₄s and, therefore, this was not considered to be an inhibited population.

**Site C - Klamath Falls**

Climatological data for April, 1985 and June and July, 1986 were not available from Round Grove. The mean monthly maximum air temperature fluctuated about the 29 year average more so than the minimum. September and November, 1985 and September, 1986 were all approximately 5 C below normal and April, 1987 was about 6 C above normal. Only January, 1986 showed a substantial deviation in the minimum air temperature (6 C above). Substantial deviations in the total monthly precipitation were only below normal and occurred during the months of January and December, 1985 and December, 1986 (5 cm each).

Overall, the total number of nematodes at this site was usually under 2000, a number smaller than that seen at either Corvallis or Langlois (Figure 13, Table 3). No discernible pattern of transmission was evident at this site. Peak abundances were seen from the fall, 1985 through the spring, 1986 with low levels of nematodes present the rest of the time. Six genera of nematodes were again encountered with *Ostertagia*, *Cooperia* and *Nematodirus* predominating (Table 3). However, two genera (*Capillaria*, *Haemonchus*) were found which had not been recovered at the other two sites and two (*Trichuris*, *Oesophagostomum*)
Figure 11. Total number of *Cooperia* spp. recovered from tracer calves at the Langlois study site (top) and percent of total represented by early-fourth stage larvae (E₄), late-fourth stage larvae (L₄) and adults (bottom).
Figure 12. Total number of Ostertagia spp. recovered from tracer calves at the Langlois study site (top) and percent of total represented by early-fourth stage larvae (E₄), late-fourth stage larvae (L₄) and adults (bottom).
Figure 13. Total number of nematodes recovered from tracer calves at the Klamath Falls site.
<table>
<thead>
<tr>
<th>Parasite</th>
<th>Sp '85</th>
<th>Su</th>
<th>F</th>
<th>W '86</th>
<th>Sp</th>
<th>Su</th>
<th>F</th>
<th>W '87</th>
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</thead>
<tbody>
<tr>
<td>Ostertagia spp. α</td>
<td>33</td>
<td>9</td>
<td>1152</td>
<td>3041</td>
<td>1446</td>
<td>15</td>
<td>273</td>
<td>174</td>
</tr>
<tr>
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<td>28</td>
<td>11</td>
<td>820</td>
<td>3000</td>
<td>1074</td>
<td>220</td>
<td>31</td>
<td>130</td>
</tr>
<tr>
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<td>10</td>
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<td>140</td>
<td>207</td>
<td>447</td>
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<td>1627</td>
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<td>73</td>
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</tr>
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<td>29</td>
<td>1</td>
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</tr>
<tr>
<td>I. axei α</td>
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<td>3</td>
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<td>7</td>
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<td>0</td>
<td>27</td>
<td>100</td>
</tr>
<tr>
<td>N. helvetianus α</td>
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<td>7</td>
<td>80</td>
<td>7</td>
<td>20</td>
<td>7</td>
<td>13</td>
<td>60</td>
</tr>
<tr>
<td>N. spathiger α</td>
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<tr>
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</tr>
</tbody>
</table>

*Sp = spring; Su = summer; F = fall; W = winter.

1α = early-fourth stage larvae.

2E = late-fourth stage larvae.
recovered at Corvallis and Langlois were not present at Klamath Falls. Cumulatively, *Ostertagia* was the most abundant nematode present followed by *Cooperia*.

Seasonally, *Nematodirus* was virtually absent in the summers with the abundance then increasing somewhat each of the subsequent falls (Figure 14). Early-fourth stage larvae were encountered only once, during the winter, 1986 and were present in proportions indicating inhibition.

The numbers of *Cooperia* at Klamath Falls were consistently low during the spring of each year. This was followed by an increase in the fall or winter when the major peaks of transmission occurred. No E₄s of *Cooperia* were encountered during the study at this site.

*Ostertagia* exhibited no discernible pattern of transmission at this study site (Figure 16). Peak abundance occurred from the fall, 1985 through the spring, 1986. Early-fourth stage larvae in proportions indicating inhibition were recovered during this same time period as well as the fall, 1986 and possibly winter, 1987.

Site D - Fort Rock

Climatological data for the month of July, 1985 were not available from the Silver Lake Ranger Station. The mean monthly minimum air temperature only showed substantial deviations below normal, occurring during the months of January, November and December, 1985 (5 C each). Mean monthly maximum air temperature was 5 C above normal in April, 1985 and 5 C below normal in September, 1985 and 1986. Although total monthly precipitation did not deviate substantially from the 17 year average, it was consistently slightly below normal except in September, 1985, February, May, June and September, 1986.

The total numbers of nematodes encountered in tracer calves from this site was equivalent to Klamath Falls and smaller than either Corvallis and Langlois. No seasonal pattern of transmission was evident here (Figure 17). Six genera of nematodes were also recovered from the tracers with *Ostertagia*, *Cooperia* and *Nematodirus* predominating (Table 4). *Haemonchus* was found to be present as it had been at Klamath
Figure 14. Total number of *Nematodirus* spp. recovered from tracer calves at the Klamath Falls study site (top) and percent of total represented by early-fourth stage larvae (E₄), late-fourth stage larvae (L₄) and adults (bottom).
Figure 15. Total number of *Cooperia* spp. recovered from tracer calves at the Klamath Falls study site (top) and percent of total represented by early-fourth stage larvae (*E₄*), late-fourth stage larvae (*L₄*) and adults (bottom).
Figure 16. Total number of *Ostertagia* spp. recovered from tracer calves at the Klamath Falls study site (top) and percent of total represented by early-fourth stage larvae (E₄), late-fourth stage larvae (L₄) and adults (bottom).
Figure 17. Total number of nematodes recovered from tracer calves at the Fort Rock study site.
Table 4. Species composition and abundance of nematodes recovered from tracer calves at the Fort Rock study site.

<table>
<thead>
<tr>
<th>Parasite</th>
<th>Sp '85</th>
<th>Su</th>
<th>f</th>
<th>W '86</th>
<th>Sp</th>
<th>Su</th>
<th>f</th>
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<tr>
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<td>O. ostertagii</td>
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<td>9</td>
<td>1887</td>
<td>213</td>
<td>319</td>
<td>59</td>
<td>065</td>
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<td>O. lyrata</td>
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<td>0</td>
<td></td>
<td>7</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Teladorsagia circumcincta</td>
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<td>0</td>
<td></td>
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<td>19</td>
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<td>1</td>
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<td>0</td>
<td>143</td>
<td>0</td>
<td>1</td>
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</tr>
<tr>
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<td>0</td>
<td>1327</td>
<td>7</td>
<td>1493</td>
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<td>500</td>
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<tr>
<td>C. oncophora</td>
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<td>1000</td>
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<td>1100</td>
<td>167</td>
<td>1200</td>
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<tr>
<td>C. surinamensis</td>
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<td>0</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>13</td>
<td>27</td>
<td>0</td>
</tr>
<tr>
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<td>0</td>
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<td>40</td>
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<tr>
<td>Trichostrongyulus spp.</td>
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<td>6</td>
<td>7</td>
<td>1</td>
<td>80</td>
<td>1</td>
<td>3</td>
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<td>T. axei</td>
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<td>0</td>
<td>1</td>
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<td>8</td>
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<td>0</td>
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<tr>
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<td>0</td>
<td>0</td>
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<tr>
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<td>0</td>
<td>220</td>
<td>13</td>
<td>3800</td>
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<td>57</td>
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<td>N. helvetianus</td>
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<td>1033</td>
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<td>47</td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>80</td>
<td>0</td>
</tr>
<tr>
<td>N. filicollis</td>
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<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<tr>
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<td>173</td>
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<td>1</td>
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</tr>
</tbody>
</table>

Sp = spring; Su = summer; f = fall; W = winter.

1st = early-fourth stage larvae.
2nd = late-fourth stage larvae.
Falls. *Trichuris* was again present as it had been at Corvallis and Langlois. Neither *Capillaria* nor *Oesophagostomum* were recovered at this site.

On a cumulative basis, *Nematodirus* was the most abundant followed by *Ostertagia*. However, the pattern of abundance for *Nematodirus* was not clear (Figure 18). A wide range in abundance existed throughout the study. Yet, unlike Klamath Falls, the abundance of *Nematodirus* was high in the summer followed by decreases in the fall. Early-fourth stage larvae were encountered often; however, proportions indicating inhibition were present only during the fall, 1985 and winter and spring, 1986. Although the proportions of E₄,s and L₄,s present in the summer, 1986 were similar the E₄,s did outnumber the L₄,s possibly indicating inhibition during this time as well.

The abundance of *Cooperia* was also variable (Figure 19). No seasonality was apparent although the abundance in the summer and winter exceeded both the spring and fall. Very few E₃,s were encountered and never in proportions which indicated inhibition.

The overall abundance of *Ostertagia* was generally low (Figure 20). On a seasonal basis, fall had the lowest numbers present followed by increases in the winter and fairly constant numbers in the spring and summer. Very few E₃,s were encountered and in proportions only slightly indicative of inhibition.
Figure 18. Total number of Nematodirus spp. recovered from tracer calves at the Fort Rock study site (top) and percent of total represented by early-fourth stage larvae (E₄), late-fourth stage larvae (L₄) and adults (bottom).
Figure 19. Total number of Cooperia spp. recovered from tracer calves at the Fort Rock study site (top) and percent of total represented by early-fourth stage larvae ($E_4$), late-fourth stage larvae ($L_4$) and adults (bottom).
Figure 20. Total number of *Ostertagia* spp. recovered from tracer calves at the Fort Rock study site (top) and percent of total represented by early-fourth stage larvae (E₄), late-fourth stage larvae (L₄) and adults (bottom).
DISCUSSION

Of the four study sites, the climates at both Langlois and Corvallis were the most moderate with high amounts of precipitation most of the year (Figures 1, 2). Such climates are quite conducive to parasite survival and transmission and this is reflected by the high numbers of parasites present at these two sites (Tables 1, 2; Figures 5, 9). At Corvallis, a distinct seasonality in parasite abundance was evident with peak abundances occurring in fall and winter. This, along with the lower abundances during spring and summer corresponds well with the pattern of precipitation in this area. At Langlois, the numbers of nematodes were more constant over all seasons. This constancy may be associated primarily with the more moderate temperature at Langlois than at Corvallis, although abundance did decrease over the summer when precipitation decreased.

Seasonal patterns of total nematode abundance at either Klamath Falls or Fort Rock were not evident during the study (Figures 13, 17). At Klamath Falls, abundances were fairly low and constant except during fall, 1985 through spring, 1986. At Fort Rock, abundances were always low in the fall but fluctuated considerably during the other seasons. The low numbers in the fall correspond to the period of time the cattle were grazing hay aftermath, a field which had not been grazed since the previous year. Such pastures are usually considered to be safe (see Williams et al., 1986) and thus may account for the decreased nematode abundance at Fort Rock during the fall. The lack of distinct patterns of transmission at both Fort Rock and Klamath Falls may be a reflection of the harsh winters and the summer irrigation used on the pastures. This may also be responsible for the overall lower abundance at these two sites compared to Corvallis and Langlois.

Four genera of nematodes were commonly found at all four study sites. Of these, *Ostertagia*, *Cooperia* and *Nematodirus* comprised the bulk of the populations. Variations in which genus predominated were evident between study sites as well as seasons of the year. On a cumulative basis, *Ostertagia* was the most abundant genus present at
Klamath Falls. This genus predominated throughout the study except during the first spring. Cumulatively, *Nematodirus* was the most abundant at Langlois and predominated throughout the study at this site except during winter. *Ostertagia* became the most abundant nematode genus at that time. *Nematodirus* was also cumulatively the most abundant genus found at Fort Rock. However, it only predominated during the summer and fall with *Ostertagia* then becoming predominant during the winter. In the spring, either *Nematodirus* or *Ostertagia* was the most abundant. At Corvallis, *Cooperia* had the highest overall total numbers. However, it was the predominant genus only during the fall. In the winter and spring, numbers of *Cooperia* approximated or were slightly less than *Ostertagia* with both then becoming subordinant to *Nematodirus* during the summer.

The species composition of the nematodes varied somewhat between sites and was influenced primarily by the presence of other ruminant species. Cattle at the Langlois and Fort Rock sites both have contact at some point with pastures grazed by sheep and this was reflected in the species composition of their nematode fauna. *Nematodirus spathiger, N. abnormalis, N. filicollis, N. battus* and *Teladorsagia circumcincta* are all parasites typical of sheep which were found in the tracer calves (Tables 2, 4). At Langlois, continual introductions of the sheep nematodes by cattle returning from the secondary ranch probably occurs each year. However, the recovery of these species of nematodes from tracer calves which did not have direct contact with the sheep indicates they are completing their life cycles and are being perpetuated on the pastures at the primary ranch. Although most of the sheep nematodes listed are not considered to be pathogenic for cattle, *N. battus* may be an exception. This parasite is the most pathogenic sheep nematode occurring in Great Britain (see Dunn, 1978) which was only recently introduced into the U.S. (Hoberg et al., 1986). It has long been known that cattle can acquire and maintain infections of this parasite even in the absence of sheep (Parfitt and Michel, 1958; Helle, 1981; Bairden and Armour, 1987; Coop et al., 1988; Rickard et al., 1989). However, recent clinical cases of nematodiriasis attributed to *N. battus* in calves have
been recorded (Armour et al., 1988). Therefore, buildup of this nematode on cattle pastures may have detrimental effects on the calves grazing those pastures.

The recovery of *Ostertagia leptospicularis* from a tracer calf in the winter, 1987 is worth noting. This parasite is thought to be more typical of cervids (see Rickard and Zimmerman, 1986) but will infect goats, sheep and cattle (Bisset, 1980; Borgsteede, 1981). In cattle, clinical ostertagiasis is much more severe when *O. leptospicularis* comprises part of the *Ostertagia* population present (Al Saqur et al., 1980; 1982a,b; 1984). There is also evidence that *O. ostertagi* and *O. leptospicularis* are differentially susceptible to anthelmintics which can lead to increased populations of the latter species (see Al Saqur et al., 1980; Lichtenfels, personal communication). The finding of *O. leptospicularis* in this tracer calf as well as *O. kolchida* and *O. leptospicularis* in other animals from Newberg, Oregon (Rickard and Zimmerman, 1986; Mulrooney et al., unpublished data) would indicate this parasite species complex is becoming an established part of the nematode fauna of cattle in this area.

The only species of *Oesophagostomum* recovered from tracer calves was *O. venulosum*. While this nematode is generally recognized as a parasite of sheep and cervids (Levine, 1980; Borgsteede, 1981) recent work suggests it may supplement or replace *O. radiatum* in cattle in the western U.S. (Padilha-Charles, 1985; Baker and Fisk, 1986; Hoberg et al., 1988). Recovery of exclusively *O. venulosum* in the present study would support this. Probable sources of infection for cattle are sheep and black-tailed deer. At Corvallis, deer are quite numerous in the area where the study occurred while at Langlois, both sheep and deer may be reservoirs for this parasite species.

The primary periods of transmission for *Nematodirus* were somewhat different for each study site. Although both Langlois and Corvallis showed fairly steady transmission throughout the year (Figures 6, 10), a trend toward increasing numbers from spring through the summer and/or fall was evident at Corvallis. Overall numbers at Klamath Falls were too low to detect any seasonal pattern of transmission. However, this
parasite was virtually absent in the summers with some amount of increase in abundance in the fall (Figure 14). In contrast, Fort Rock had high numbers of Nematodirus present in the summer. The high numbers present at Fort Rock as well as the increasing numbers at Corvallis in the summer are unusual as Nematodirus is generally low or absent during the summer (Randall and Gibbs, 1977; Baker and Fisk, 1986; Baker et al., 1981, 1984).

 Arrested development is considered to be a normally occurring feature of nematode life cycles which evolved when confronted by adverse environmental conditions not conducive to their survival or transmission. This phenomenon would be of importance in areas such as the extreme range of a parasite's distribution where the external environment barely permits its existence (see Gibbs, 1986). However, in parasites such as Nematodirus which are well adapted to colder climates (Rose, 1966; Smith, 1972; Gibbs, 1979, 1980) the value of arrested development in the winter in such areas is unclear. In fact, given that egg development and larval survival at higher temperatures (as experienced during the summer in the Northern U.S. and year-round in the southern U.S.) is poor for Nematodirus, one might expect to see little or no transmission with possible larval inhibition during this time. Such is the case in parts of the southern U.S. where Nematodirus is essentially absent from the parasite fauna of cattle (Craig, 1979; Williams et al., 1987). However, in Oregon this did not prove to be true. Arrested development of Nematodirus was detected at all study sites and occurred during the fall and/or winter. This timing of inhibition was the same as seen in the northern regions of the U.S. where this phenomenon also occurs (Smith, 1974; Randall and Gibbs, 1977; Baker et al., 1981). Factors other than strictly environmental influences as proposed by Smith (1974) must be partially responsible for induction of hypobiosis in this parasite.

 Of the nematodes present in the tracer calves, Cooperia exhibited the most seasonally defined pattern of transmission. Peak abundances occurred during the fall and winter at Corvallis, Langlois and Klamath Falls (Figures 7, 11, 15). The reduced numbers of Cooperia found at
Klamath Falls during the winter, 1987 may have been a result of the tracer calves grazing at the home ranch rather than the border ranch. The overall abundance of Cooperia at Fort Rock was quite variable with no seasonally defined pattern apparent (Figure 19). The observation of peak transmission for Cooperia in the fall and winter at Corvallis extends those made by Syhre et al. (1987) working in the same area. The seasonality seen in the present study is similar to those patterns seen elsewhere in the U.S. (Randall and Gibbs, 1977; Baker et al., 1981, 1984; Williams et al., 1983).

The presence of hypobiotic larvae of Cooperia was variable. Inhibited larvae were present at both sites west of the Cascade Mountains (Figures 7, 11) while they were absent at both sites east of the Cascades (Figures 15, 19). When present, hypobiosis occurred during the fall and/or winter. Again, the timing of this phenomenon was similar to that seen in other regions of North America (Smith, 1974; Randall and Gibbs, 1977; Craig, 1979; Baker et al., 1981; Williams et al., 1983, 1987). The presence of hypobiotic larvae in one area of a state and the lack of such in another area as seen in this study also occurs in California (Padilha-Charles, 1985; Baker et al., 1981, 1984; Baker and Fisk, 1986). Previous work has indicated environmental factors are primarily responsible for the induction of developmental arrest of larval Cooperia. For example, Smith (1974) allowed three parasite-naive calves to graze contaminated pastures for 2 week periods during the fall. The results showed larval Cooperia underwent arrested development during this time with the percentage of the total arrested Cooperia present increasing as time progressed. He concluded that developmental arrest was correlated with decreasing temperatures and photoperiod. The works of Michel (1974, 1978) have supported this conclusion. Interestingly, comparisons of the climatologic data shows one of the two areas in California lacking developmental inhibition of Cooperia was climatologically similar to those areas in Oregon also lacking inhibition; however, the area in the Sacramento Valley in which arrested development did occur was climatologically most similar to Fort Rock and Klamath Falls in terms of precipitation and Corvallis in terms
of temperature. Baker and Fisk (1986) proposed that the size of the population of *Cooperia* may be important in the induction of arrested development, thus explaining its lack in some areas and presence in others. Both Klamath Falls and Fort Rock had relatively low numbers of *Cooperia* and lacked inhibition. Corvallis had relatively high numbers during the fall and winter with inhibition present at this time. Langlois had relatively low numbers the first year and inhibited development was also lacking. However, when the numbers increased the fall of the second year, developmental inhibition also occurred. This data supports the proposal of Baker and Fisk (1986) and indicates the size of the population may be the primary factor influencing developmental inhibition in this genus.

In North America, *O. ostertagi* is recognized as the most pathogenic and economically important nematode of cattle (see Williams, 1986). Epizootiologically studies over the past 15-20 years have shown two distinct patterns of transmission exist for this parasite. In northern regions with intense winters and mild summers, peak transmission of *Ostertagia* occurs in the summer and fall. Acquisition of inhibited prone larvae occurs during the fall and numbers remain high over the winter. These inhibited larvae then resume development from late winter into spring. Larvae on pastures are low in the spring and, therefore, new infections are generally not acquired by grazing cattle at this time. However, numbers increase over the summer and infections increase also. The highest levels of infection usually occur late summer through fall. Type I ostertagiasis would occur from summer into fall and Type II from winter into spring. Larval inhibition in the winter has been documented in Maine (Randall and Gibbs, 1977), Michigan (Schillhorn van Veen and Melancon, 1984), Ohio (Herd, 1980), Idaho (Gibbs, 1979), Washington (Malczewski et al., 1975), the northern coast of Oregon (Kistner et al., 1979) and implicated indirectly in Kentucky (Lyons et al., 1981).

In contrast to the northern temperate regions, the southern regions have a different pattern. Peak transmission occurs during winter and spring. Although acquisition of inhibition prone larvae may occur
during the fall and winter, the greatest levels are reached in the spring. Transmission then decreases over the summer with inhibited larvae acquired in the spring making up the bulk of the population present. These larvae resume development over the summer through the fall. Type I ostertagiasis would be expected to occur from winter into spring and Type II from late summer into fall. Larval inhibition in the spring has been documented in Texas (Craig, 1979), Louisiana (Williams et al., 1983, 1987), Georgia (Ciordia et al., 1971), Missouri (Brauer, 1983), Florida (Courtney), California (Padilha-Charles, 1985; Baker and Fisk, 1986; Baker et al., 1981, 1984) and implicated indirectly in Oklahoma (Schillhorn van Veen and Melancon, 1984).

In the present study, marked differences occurred in the pattern of transmission of Ostertagia with none of the data fitting the typical northern or southern pattern. At Corvallis, peak transmission occurred in late fall and winter (Figure 8). This time period is between that seen in both the northern regions (summer-fall) and southern regions (winter-spring). At Langlois, peak transmission also occurred during the fall and winter with possible extension into the spring (Figure 12). This is also a modification of the typical northern and southern pattern. At Fort Rock, transmission was lowest in the fall and increased in the winter (Figure 20) a pattern more associated with southern temperate regions. At Klamath Falls, no discernible pattern of transmission was evident (Figure 16).

Differences in the onset and timing of arrested development of Ostertagia was also evident. At Corvallis, the fall and winter inhibition seen (Figure 8) correlates to the northern pattern defined above. Hyphobiosis present in the fall or winter at Fort Rock (Figure 20) also correlates with this pattern. At Klamath Falls, inhibition was more extensive being present in the fall, 1985 through spring, 1986 and again in the fall, 1986 and possibly winter, 1987 (Figure 16). This is reminiscent of the southern pattern in which inhibition can occur in the fall and winter but is highest in the spring. These data indicate that, as for the northern coastal area of Oregon (Kistner et al., 1979), Type II ostertagiasis may occur late winter through spring in the Willamette
Valley of western Oregon and parts of central Oregon. For parts of south-central Oregon, Type II ostertagiasis may occur in the summer.

The apparent absence of arrested development at Langlois (Figure 12) has two possible explanations. First, the time period in which inhibition prone larvae are acquired may be very short. As the experimental design required placing tracer calves onto pasture once during each of the four seasons, it is possible this window of time was missed. The presence of E_s in fall, 1985 may indicate that the tracer calves were grazing when the tendency for hypobiosis was only just beginning or ending. The alternative to this is that larval inhibition does not occur in this area of Oregon. As the moderate climate is well within the extremes in which Ostertagia can survive (Goldberg and Rubin, 1956; Bell et al., 1960; Rose, 1961, 1970; Schwink, 1963; Ciordia and Bizzell, 1963; Pandey, 1972a,b) the stimulus for arrested development may not be as great as in other regions with more fluctuating climates. The presence of E_s in the fall, 1985 may be a result of the abnormally low precipitation present at Langlois during most of 1985. Although there is no evidence in the literature to support the ability of Ostertagia to turn on and off hypobiosis in different years, there is evidence of strain differences in which one strain has more of a propensity to undergo hypobiosis than the other (Armour et al., 1967a,b; Michel, 1967a,b; Sollod, 1967). Further support for this proposal comes from Frank et al (1986, 1988) who transferred Ostertagia from Ohio (winter inhibition) to Louisiana and from Louisiana (summer inhibition) to Ohio. The results showed that the northern isolate exhibited a greater degree of hypobiosis in the northern fall while the southern isolate exhibited a marked degree of hypobiosis in the spring at both locations. These data were explained by the presence of appropriate stimuli in the north but not the south for fall hypobiosis and the presence of appropriate stimuli in both locations for spring hypobiosis. In the present study, the presence of abnormally low precipitation may have provided selection pressure for an inhibition prone strain. When precipitation remained normal over the course of the following year, this selection pressure was obviated and normal development of
Ostertagia to the adult stage occurred.

The inability to categorize the transmission patterns of Ostertagia as well as the lack of inhibition on the southern Oregon coast suggests Oregon, as a whole, is a transition zone between the typical northern and southern patterns evident elsewhere. Further research on the epizootiology of cattle nematodes in these areas is necessary in order to more fully evaluate the transmission patterns and help formulate adequate control measures.
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