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GASTROPOD INTERMEDIATE HOSTS OF LUNGWORMS (Nematoda:Protostrongylidae) ON A BIGHORN SHEEP WINTER RANGE: ASPECTS OF TRANSMISSION

by

Leslie A. Robb

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled GASTROPOD INTERMEDIATE HOSTS OF LUNGWORMS (NEMATODA:PROTOSTRONGYLIDAE) ON A BIGHORN SHEEP WINTER RANGE: ASPECTS OF TRANSMISSION submitted by LESLIE ROBB in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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ABSTRACT

Protostrongylus stilesi/rushi lungworms have been implicated as playing a major role in the bighorn sheep/lungworm/pneumonia complex. Many studies have examined the bighorn sheep aspect of the lungworm life cycle, but few studies have examined the terrestrial snail intermediate hosts. Transmission of lungworms to bighorn sheep is believed to occur in aspen copses on bighorn sheep winter range, however, the spatial and temporal aspects of transmission are unclear.

Seven species of terrestrial snails were found infected with *Protostrongylus* type larvae; the major intermediate hosts were *Vertigo gouldi*, *V. modesta*, and *Euconulus fulvus*. The prevalence of third-stage (infective) larvae in these species was highest during autumn and spring coinciding with bighorn sheep use of the winter range. Over-winter survival of the infective snails, and stability of the snail host populations, suggest that the presence of snails with infective larvae is relatively constant throughout the year. Lungworm transmission to bighorn sheep probably occurs during both autumn and spring and may not favour one particular season.

The presence of at least one other similar protostrongylid species (the mule deer lungworm *Orthostrongylus macrotis*) complicates any study of the

transmission of bighorn sheep lungworm. Although the presence of mule deer lungworm is an inherent problem, several aspects of bighorn sheep behaviour, their high population density and high production of first stage larvae while on the winter range, suggest that many of the infected snails from the winter range harboured P. stilesi/rushi lungworm.

Observations of bighorn sheep during the autumn indicated that they often used the edge areas of aspen copses. Lungworm availability values were highest in aspen edge and grass-edge aspen copses habitats during autumn, and aspen-center and aspen-edge habitats during spring.

Rate of larval development in naturally-infected intermediate hosts may differ from that reported for snails infected in the laboratory. Inactivity of laboratory-infected snails seems to extend the rate of larval development beyond what would be predicted if temperature were the only factor affecting the rate of larval development.

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I would like to express sincere thanks to the members of my supervisory committee, Drs. W.M. Samuel, J.C. Holmes, D.A. Boag, W.D. Wishart, and J.R. Spence, for their suggestions and comments throughout this study. I sincerely thank my supervisor, Dr. W. M. Samuel, for providing me with the opportunity to pursue this research. His comments and editorial criticisms were extremely helpful. I wish to extend special thanks to Dr. D.A. Boag for allowing me to use his gastropod data from Sheep River, this project could not have been completed without his assistance. I would like to thank Dr. J.C. Holmes for providing the funding that allowed me to conduct sheep observations.

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INTRODUCTION

Localized die offs of Rocky Mountain bighorn sheep (Ovis canadensis canadensis) frequently occur throughout their range (see reviews by Buechner, 1960; Forrester and Senger, 1963; Stelfox, 1971). Although numerous factors may be involved in such population declines, a poorly understood respiratory disease complex may play a major role (Buechner, 1960; Forrester and Senger, 1963; Forrester, 1971; Hibler et al., 1982; review by Lawson and Johnson, 1983). The least complicated hypothesis suggests that nematode lungworms Protostrongylus stilesi and/or Protostrongylus rushi (Nematoda:Metastrongyloidea) predispose bighorn sheep lungs to colonization by opportunistic bacteria, such as Pasteurella spp., which aggravates the development of a contagious virulent pneumonia. The impact of a pneumonia infection is demonstrated by Pasteurella hemolytica biotype I that has been found to cause mortality in experimentally infected bighorn sheep in as little as 16 hours post infection (Onderka, 1986).

Protostrongylus stilesi/rushi lungworms are common parasites of North American bighorn sheep (Becklund and Senger, 1967; Forrester, 1971; Uhazy et al., 1973). A high proportion of heavily infected individuals may characterize a herd in poor condition, and possibly in danger of a die-off (Uhazy et al., 1973). Bighorn sheep can be subjected to

Various stress factors, such as severe winter weather, competition with wapiti (Cervus elaphus) and deer (Odocoileus spp.), deteriorated range condition, and high bighorn sheep density (see review by Stelfox, 1971). How these factors interact, and to what degree they contribute to a bighorn sheep die off, is unknown.

Lungworm infection of bighorn sheep is believed to occur on sheep winter range (Uhazy et al.,1973; Hibler et al., 1982; Boag and Wishart, 1982). Several factors support this premise:

1) Peak production of first-stage larvae by Protostrongylus spp. lungworms infecting bighorn sheep occurs during late winter when sheep are still on their winter range (Forrester and Senger, 1964; Uhazy et al., 1973; Jorgenson and Wishart, 1982; Festa-Bianchet, 1982).

2) Sheep herds often congregate for extended periods when on their relatively small winter range, likely increasing the probability of sheep lungworm infection (Uhazy et al, 1973).

3) Snail populations are predominately associated with organic litter (Burch, 1955; Locasciulli and Boag, 1987) and potential lungworm intermediate host snail species in Alberta show a preference for litter with deciduous content (Boag and Wishart, 1982; Kralka, 1986; Locasciulli and Boag, 1987). Thus, aspen copses on winter range should be more favourable for snails than the alpine meadows on summer range.

4) Gastropods are most active during moist conditions (Boycott, 1934; Crawford-Sidebotham, 1972; Skorping, 1982), as well, first stage larvae likely require moisture to actively infect a gastropod intermediate host (Lankester and Anderson, 1968; Skorping, 1982). Environmental conditions favourable for snail and larval activity commonly occur on winter range coinciding with bighorn sheep presence.
5) Finally, the immune system in bighorn sheep may influence the 'success' of lungworm infection (Festa-Bianchet, 1987). Sheep in poor condition, with depressed immune systems, might be more susceptible to lungworm infection than healthy sheep. Harsh winters, further complicated by a high sheep population and poor quality range, may weaken the condition of some individuals, rendering them susceptible to lungworm infection in the spring.

A current hypothesis regarding lungworm transmission to bighorn sheep has been proposed by Boag and Wishart (1982). They hypothesized that: 1) lungworm transmission to bighorn sheep occurs on the winter range; 2) aspen copses on winter [redacted]e are major sites of snail infection during spring; 3) snail populations are most abundant on winter range during late summer - early autumn; and 4) lungworm transmission to bighorn sheep occurs primarily during late summer - early autumn when sheep return to their winter range. The Boag/Wishart hypothesis of an autumn transmission period is supported by Samson and Holmes (1985) who determined that

development rates of P. stilesi/rushi in the snail intermediate host are temperature dependent. They applied temperature dependent developmental rates to known temperatures in aspen copses on a bighorn sheep winter range and concluded that, because of probable rapid larval development during summer, the proportion of snails with infective larvae would be highest during autumn. However, little is known about the snail intermediate host species or the rate of larval development in 'field' snails. Thus, before the temporal and spatial aspects of lungworm transmission to bighorn sheep can be further clarified, examination of the postulations made by Boag and Wishart (1982) regarding gastropod lungworm transmission is necessary.

Timing of P. stilesi/rushi transmission is probably affected by the rate of larval development in snail intermediate hosts. Kassai (1958) believed that the most important factors affecting development of protostrongylid larvae were: "1) the temperature of the environment, 2) the snail species of the intermediate host, 3) the individual properties of the snail, and 4) the individual properties of the larvae (vitality)". Subsequently, researchers have examined factors influencing rate of larval development in various parasite systems.

Many species of protostrongylid larvae demonstrate a temperature dependent rate of development; rate of larvae

development increases with increasing temperature (Rose, 1957; Lankester and Anderson, 1968; Halvorsen and Skorping, 1982; Samson and Holmes, 1985). However, during warm and dry conditions in the summer, many snail species estivate, a behaviour characterized by withdrawal into the shell and cessation of activity (Newell and Appleton, 1979). For Protostrongylus spp. larvae, summer is the time when ambient temperatures should promote a rapid rate of larval development (Samson and Holmes, 1985). What effect estivation of snail hosts has on development of Protostrongylus spp. is unknown. Additionally, factors such as the species of intermediate host (Yousif and Lammler, 1975; Skorping and Halvorsen, 1980; Urban, 1980), intensity of larval infection, and gastropod size and nutritional status (Skorping, 1984) have been shown to influence the rate of protostrongylid larval development.

Some parasite intermediate host species exhibit altered behaviour, which may facilitate transmission of the parasite to its definitive host (Holmes and Bethel, 1972). Samson (1984) concluded that of the strategies outlined by Holmes and Bethel (1972), disorientation and altered responses of the intermediate host were the most applicable to the snail-bighorn sheep system of lungworm transmission. She found no differences in attraction to leaf litter, temperature, or light intensity preferences, for uninfected Vallonia pulchella and those infected with P. stilesi/rushi.

However, she did find that infected snails were generally more active than uninfected snails, and concluded that infected snails were less likely to become trapped in unfavourable areas. If activity differs between infected and uninfected snails under natural situations, infected snails may be more prevalent at certain times and/or locations on the winter range than uninfected snails.

Knowledge of the lungworm life cycle is paramount to understanding the bighorn sheep respiratory disease complex. First-stage larvae are passed in sheep faeces after which they infect gastropod intermediate hosts, and develop to the infective third-stage larvae. Completion of the life cycle occurs by two pathways: 1) presumed accidental ingestion of infected gastropods by sheep; and 2) transplacental transmission when a pregnant ewe accidentally ingests an infected gastropod and the larvae are transmitted to the fetus (see review by Forrester, 1971). Little is known about either mode of transmission and it is unclear if one pathway is more "prevalent" for the parasite than the other. Samson et al. (1987, in press) noted transplacental transmission of lungworm in 21 of 44 free-ranging bighorn lambs at Ram Mountain, Alberta, suggesting that in some bighorn sheep herds, this mode of transmission may be a common strategy of lungworm infection. Irrespective of the role transplacental transmission plays in establishing lungworms, first-stage larvae develop to the infective

third stage in a gastropod intermediate host; thus larval development in gastropods is critical to completing the life cycle.

Despite the important role gastropod intermediate hosts play in the bighorn sheep/lungworm life cycle, most research has concentrated on the pathogenic effects of lungworms on bighorn sheep. Few studies have attempted to identify the snail intermediate host species and determine the temporal and spatial aspects of bighorn sheep lungworm transmission. The major objective of this study was to examine postulations made by the Boag/Wishart hypothesis regarding gastropod transmission of P. stilesi/rushi to bighorn sheep on the winter range.

Several objectives were addressed in an attempt to clarify lungworm transmission to bighorn sheep on their winter range:

1) monitor the presence and developmental stages of Protostrongylus stilesi/rushi infecting gastropods on the Sheep River winter range to determine a likely time for lungworm transmission to bighorn sheep,

2) monitor the frequency of infection by Protostrongylus spp. in gastropods collected from aspen copse and grass meadow habitats to determine whether or not transmission areas are site specific,

3) determine the effect of three different moisture regimes on the rate of P. stilesi/rushi development in the laboratory intermediate host, Vallonia pulchella, and,

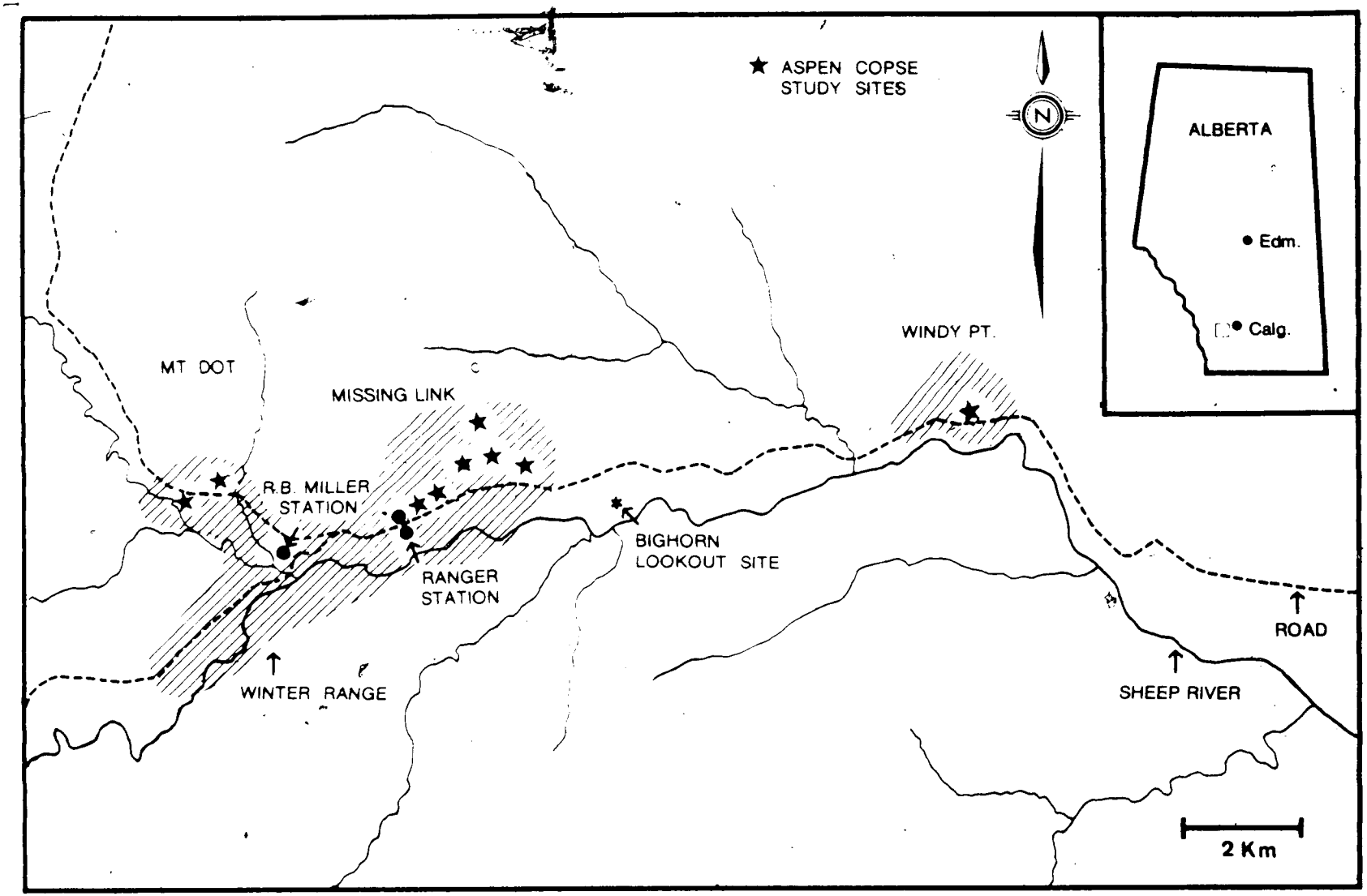
4) identify the predominant species of protostrongylid parasites infecting snail intermediate hosts on the bighorn sheep winter range.

MATERIALS AND METHODS

Collection and examination of terrestrial gastropods

This research was done at the Sheep River Wildlife Sanctuary (50° 40'N, 114° 35'W), 27 km west of Turner Valley, Alberta (Fig. 1). The Sanctuary is a winter range and the bighorn sheep migrate between summer and winter ranges (Festa-Bianchet, 1986). The resident herd of approximately 160 sheep predictably leaves the winter range between 13 - 19 May (earliest and latest median dates, Festa-Bianchet, 1986) and returns between 6 Sep. - 7 Oct (median dates, Festa-Bianchet, 1986). The two ranges differ; summer range is located to the west of the Sanctuary in alpine meadows above tree line (1500 - 2450m), and winter range is comprised of grass meadows and aspen-copses below tree line (1450 - 1700m) (Festa-Bianchet, 1986). Gastropods are numerous in aspen copses on the Sheep River winter range (Boag, 1982; Boag and Wishart, 1982; Locasciulli and Boag, 1987). In addition, migratory movements, herd condition, and lungworm larvae output of the resident bighorn sheep have been studied intensively from 1978 to 1987 (Festa-Bianchet, 1982; 1983; 1986; 1987). The population work on gastropods, knowledge about the bighorn sheep herd, and accessibility of the Wildlife Sanctuary, made the Sheep River area an ideal location for a study of gastropod

Figure 1. Location of the Sheep River Wildlife Sanctuary in Alberta, and the locations of the nine aspen copse study sites located in the Sanctuary.


ASPEN COPSE
STUDY SITES
N
ALBERTA
Edm.
Calg.
WINDY PT.
MT DOT
MISSING LINK
R.B. MILLER
STATION
RANGER
STATION
BIGHORN
LOOKOUT SITE
ROAD
WINTER RANGE
SHEEP RIVER
2 Km

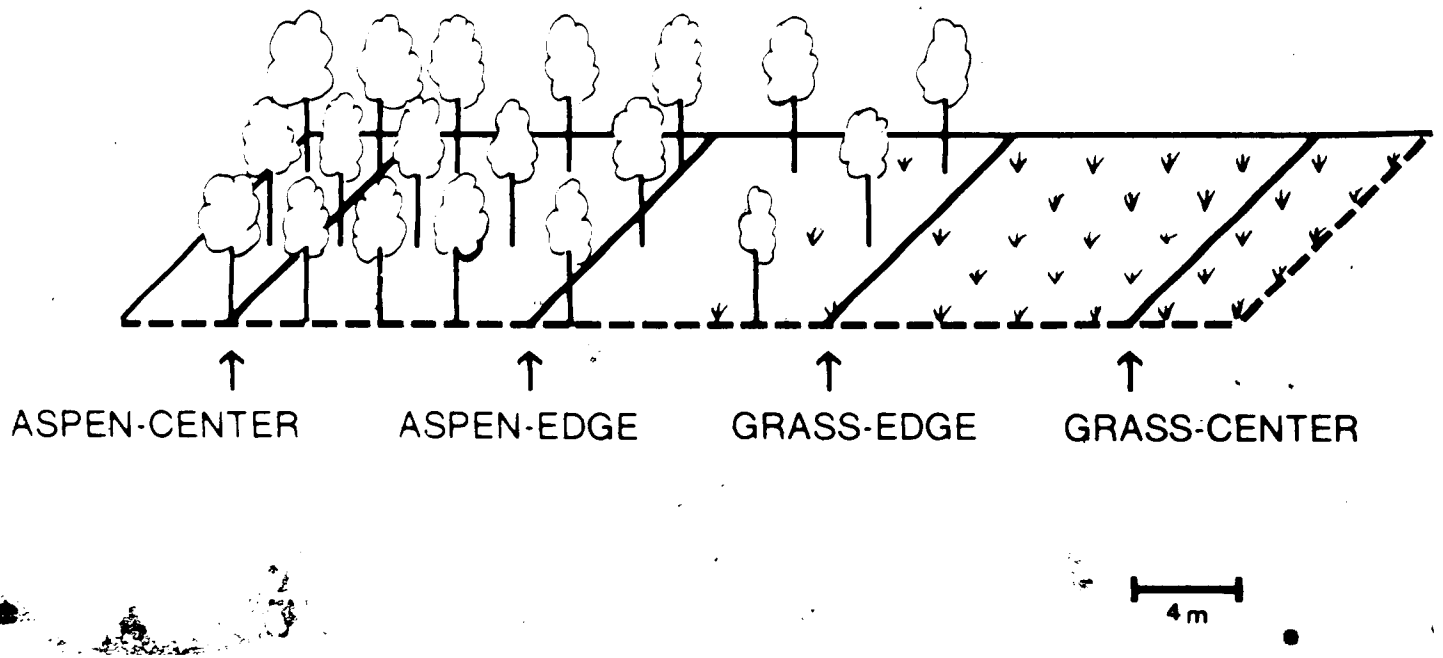
transmission of bighorn sheep lungworm.

Nine similar aspen copses were chosen from the area of the winter range extensively used by bighorn sheep; each was divided into aspen-center, aspen-edge, grass-edge, and grass-center habitat types (Fig. 2). Gastropods were collected from each of the nine aspen copse sites using two sampling techniques: 1) organic litter removal transects (Kralka, 1986), and 2) permanent plot transects (Boag, 1982). Separate 30m transects were established in each of four habitat types for the two methods, and designated as either 'litter' or 'plot' (total of eight transects for each of the nine areas). Transects were established parallel to the tree edge of an aspen copse and an attempt was made to maintain similar aspect, slope, and vegetation cover between transects of the same habitat type.

Litter transects were sampled weekly from May through September in 1984 by removing $0.05m^2$ x 5cm of organic leaf litter from three points, chosen at random, along the transect. Litter samples were returned to the laboratory and gastropods extracted by the 'cold water process' (Kralka, 1986). The gastropods collected by organic litter removal were used in analyses of snail density (number/m^2).

Permanent plot transects consisted of plywood squares, 1.25cm x 30cm x 30cm, placed along the 30m transect at 5m intervals (total of 7 squares/transect). Plots were established one month prior to commencing gastropod

Figure 2. Representative location of transects established in each of the aspen copse habitats, aspen-center, aspen-edge, grass-edge, and grass-center.


ASPEN-CENTER
ASPEN-EDGE
GRASS-EDGE
GRASS-CENTER
4 m

collection. Gastropods observed on, or under, plots were collected and examined on a weekly basis from May throughOctober 1984, and every four days from April through June 1985. Also included in this study were gastropods collected from permanent plot transects established on the winter range by Dr. D. A. Boag, University of Alberta (see Boag, 1982). These transects were variable in length, and the plots consisted of masonite squares that were similarly examined for gastropods (Boag and Wishart, 1982). Each of these permanent plot sites was classified to one of the four habitat types outlined previously. It was assumed that collected gastropods reflected those 'available' to bighorn sheep. Gastropods collected from permanent plot samples were therefore used to determine the timing and location of lungworm transmission to bighorn sheep.

Data collected from Sheep River were analyzed by month or by season. Three seasons were defined as potential transmission periods, 1) summer (16 May - 14 August), 2) autumn (15 August - ground freeze), and 3) spring (ground thaw - 15 May). Seasonal periods reflect migration of bighorn sheep to and from the winter range; sheep are present on the winter range from approximately 15 August to 15 May (Festa-Bianchet, 1986).

After collection, gastropods were kept in vials and stored a maximum of one week at 15-18^{0}C. Gastropods were examined at 25X and identified to species with the aid of

keys in Burch (1962). J. Van Es, Department of Zoology, University of Alberta, verified identifications of all species. Pupillid snails with damaged shells could not be identified to species. In such cases these snails were recorded as Vertigo spp. Width, length, number of whorls, and developmental stage (juvenile or adult) were recorded. Pupillid adults had teeth; juveniles did not. Adults of Euconulus fulvus had 3 or more whorls. The gastropods collected in 1984 were crushed between glass slides and examined for parasitic nematodes using transmitted light at 25X. Number and developmental stage of nematodes were recorded. Infected snails with third-stage larvae were defined as 'infective'. Snails that did not contain third-stage larvae were defined as 'noninfective'. Nematode larvae were then transferred with a Pasteur pipette (.05ml) to a vial containing 85% saline. After the larvae settled to the bottom of the vial the saline was removed and the larvae killed and preserved in hot glycerin-alcohol (95 parts 70% EtOH, 5 parts glycerin).

It was necessary to keep alive the infected snails collected in 1985 (Appendix I). To determine nematode infection, snails were induced to crawl freely on a moist petri dish that was then inverted under a dissecting microscope. The 'foot' was examined at 25X magnification and the number and developmental stage of all observable larvae were recorded. Snails were then separated by species

and housed in 15cm fingerbowls lined with aspen leaf litter. Fingerbowls were kept in a refrigerator at 15°C. Every two days, fingerbowls were aired for approximately one hour and misted with non-chlorinated creek water.

Daily precipitation, monitored with a rain gauge, and high/low temperature readings were recorded at the R.B. Miller Biological Station located in the Sanctuary (Fig. 1).

Identification of nematode larvae

The bighorn sheep in the Sheep River Sanctuary are infected with the lung nematodes Protostrongylus stilesi and Protostrongylus rushi (Uhazy et al., 1973), but other protostrongylids are known to infect wildlife of western Alberta. These include, Parelaphostrongylus odocoilei (mule deer, Odocoileus hemionus), Orthostrongylus macrotis (mule deer; white-tailed deer, O. virginianus), and Protostrongylus boughtoni (snowshoe hares (Lepus americanus). These protostrongylid species use gastropods as intermediate hosts (Kralka and Samuel, 1984a; Samuel et al., 1985).

An effort was made to determine if protostrongylid species other than P. stilesi/rushi occurred on this winter range. Larvae of Parelaphostrongylus odocoilei are unique and distinct from the other species in that the posterior

end has a single, dorsal spine (Ballantyne and Samuel, 1984). However, the larval stages of P. s.ilesi/rushi, O. macrotis, and P. boughtoni are morphologically similar (Kralka and Samuel, 1984b). Fresh mule deer faeces from 17 individuals were collected in April and May, 1985. Individual faecal groups were frozen until examined for larvae by a modified Baermann technique (Samuel and Gray, 1982). As well, the infected snails collected in 1985 were used to experimentally infect mule deer fawns with third-stage larvae to determine presence of O. macrotis in snail intermediate hosts on the Sheep River winter range (Appendix I). Presence of P. boughtoni on the winter range was assumed unlikely because snowshoe hares, their tracks or faeces, were never observed on the area during this study.

Preserved larvae, from infected snails collected in 1984, were allowed to clear in pure glycerin for one week after which they were prepared as temporary mounts. Total length measurements of all larvae were determined using a drawing tube and compared to those of known species. Protostrongylid-type larvae were identified by three criteria: 1) total length of first or third developmental stages; 2) presence of a straight, symmetrically tapered, pointed posterior end on the first-stage larvae, and 3) a dark, heavily ridged cuticle on the third-stage (the infective stage) larvae.

The infective larvae of P. boughtoni are shorter than

P. stilesi and/or P. rushi, but lengths of O. macrotis and P. stilesi and/or P. rushi are similar (Kralka and Samuel, 1984b). Therefore, these larvae were compared using Scanning Electron Microscopy (SEM). Known sources of first-stage O. macrotis and P. stilesi/rushi were used to infect the snail Vallonia pulchella in the laboratory following the procedures of Samson and Holmes (1985). Infective larvae were killed with hot glycerin-alcohol and dehydrated through a series of graded alcohols to 100% EtOH; they were critically-point dried, coated with gold, mounted and examined using a scanning electron microscope.

Bighorn sheep behavioural observations

From August 28 - September 15, 1985, use of habitat by bighorn sheep on winter range was observed and recorded. The specific study area extended from Missing Link Mountain to the Sheep River, and from the bighorn lookout site to Mount Dot (Fig. 1). The study area was visually segregated by habitat type into open, aspen-edge, and aspen-center areas. Behavioural observations of all observable sheep in these habitat types were conducted every two hours, from 0730 hrs to 1930 hrs, on a daily basis.

Four categories of activity were designated: 1) standing, 2) feeding, 3) moving, and 4) resting. Sheep were

recorded as either adults or lambs, except when rams and ewes were clearly distinguishable. The number and activity of bighorn sheep present in habitat areas were recorded during each behavioural observation.

The effect of moisture on *Protostrongylus stilesi/rushi* development in the laboratory host *Vallonia pulchella*

The laboratory intermediate host, *Vallonia pulchella* was used to study the effect of moisture on the rate of development of *P. stilesi/rushi* larvae. Four replicates of the experiment were completed. First-stage larvae were collected from bighorn sheep faecal pellets by a modified Baermann technique (Samuel and Gray, 1982). Approximately 15 000 first-stage larvae, suspended in tap water, were concentrated by centrifugation at 1100 rpm for 10 minutes. Larvae were then poured into a 60 x 15 mm plastic Petri dish lined with two Whatman 1 filter paper discs 7cm in diameter. Ninety snails were exposed to the larvae by allowing them to crawl for 2 1/2 hours on the moist filter paper. During the exposure period, snails observed crawling on the Petri dish lid were placed back on the filter paper. Occasionally, snails exhibited clumping behaviour. When this was noticed they were separated.

After exposure the snails were randomly divided into

three groups of 30 snails each and placed in separate fingerbowls, 15cm in diameter, to which leaf litter had been added. Three different moisture regimes were created in the fingerbowls: 1) wet (= misted with tap water every two days); 2) damp (= misted weekly); and 3) dry (= not misted). Fingerbowls were covered and kept in a 30°C incubator for the duration of the experiment.

Commencing seven days post-exposure, snails were examined every two days for parasite infection by inducing them to crawl on a moist Petri dish that was inverted under a dissecting microscope. Snail feet were observed at 25X magnification and the number and developmental stage of larvae were recorded for all individuals. Examination of the rate of larval development was conducted until the time when half of the snails in a group contained third-stage larvae.

RESULTS

Permanent plot samples yielded a total of 6653 terrestrial gastropods that were collected and examined during May - October 1984 and April - June 1985 (Table 1A and B). Litter samples yielded a total of 605 terrestrial gastropods that were collected and examined during May - Sept. 1984 (Table 2). Protostrongylid-type larvae were found in 272 gastropods, of seven species, belonging to four families; Pupillidae, Succineidae, Endodontidae, and Zonitidae.

Damage to some pupillid snails prevented species identification, in such cases these snails were recorded as Vertigo spp. Snails infected with third-stage protostrongylid larvae were defined as 'infective' snails. Snails that did not contain third-stage larvae were defined as 'noninfective'.

An index of parasite abundance (mean intensity of infection X prevalence of infection) (Leong, 1975; Margolis et al., 1982) was calculated for each intermediate host species for 1984 and 1985. To adjust for varying sample sizes between intermediate host species, a species' index of abundance value was multiplied by its percent of the total snails collected during that year (Table 3). Euconulus fulvus, Vertigo gouldi and Vertigo modesta had the highest index values during both 1984 and 1985 and, thus, were

Table 1A. Number of snails and the prevalence of protostrongylid-type larvae infecting (Infect.) gastropods collected (Col.) from permanent plots on the Sheep River study area in 1984.

Species	# Col.	# Infect.	Prevalence %	Intensity X
Suborder Orthurethra				
Family Pupillidae				
Vertigo gouldi	878	44	5.0	2.6
Vertigo modesta	1151	38	3.3	1.7
Vertigo spp.[a]	88	8	9.1	5.8
Columella spp.	84	2	2.4	2.0
Immature pupillids	153	7	4.5	1.7
Suborder Heterurethra				
Family Succineidae				
Catinella sp.	8	4	50.0	3.5
Suborder Sigmurethra				
Family Endodontidae				
Discus cronkhitei	636	4	0.6	1.2
Punctum minutissimum	1	0	0.0	0.0
Family Zonitidae				
Retinella electrina	31	0	0.0	0.0
Euconulus fulvus	605	43	7.1	3.8
Zonitoides arboreus	2	0	0.0	0.0
Vitrina alaskana	702	2	0.2	4.0
Total	4339	152	3.5	

[a]Damaged *Vertigo* snails that could not be identified to species.

Table 1B. Number of snails and the prevalence of protostrongylid-type larvae infecting (Infect.) gastropods collected (Col.) from permanent plots on the Sheep River study area in 1985.

Species	# Col.	# Infect.	Prevalence %	Intensity X
Suborder Orthurethra				
Family Pupillidae				
Vertigo gouldi	570	41	7.2	2.2
Vertigo modesta	608	17	2.5	2.2
Vertigo spp.[a]	58	0	0.0	0.0
Columella spp.	11	0	0.0	0.0
Immature pupillids	79	0	0.0	0.0
Suborder Heterurethra				
Family Succineidae				
Catinella sp.	8	2	25.0	10.5
Suborder Sigmurethra				
Family Endodontidae				
Discus cronkhitei	411	7	1.7	1.5
Punctum minutissimum	0	0	0.0	0.0
Family Zonitidae				
Retinella electrina	4	0	0.0	0.0
Euconulus fulvus	478	36	7.5	2.1
Zonitoides arboreus	6	0	0.0	0.0
Vitrina alaskana	1	0	0.0	0.0
Total	2314	103	4.4	

[a]Damaged *Vertigo* snails that could not be identified to species.

Table 2. Number of snails and prevalence of protostrongylid-type larvae in gastropods collected from litter samples on the Sheep River study area in 1984.

Species	# Col	# Infect.	Prevalence %	Intensity X
Suborder Orthurethra				
Family Pupillidae				
Vertigo gouldi	217	9	4.1	4.0
Vertigo modesta	31	2	6.4	1.5
Vertigo spp.[a]	31	1	3.2	0.0
Columella spp.	5	0	0.0	0.0
Immature pupillids	51	1	1.9	1.0
Suborder Heterurethra				
Family Succineidae				
Catinella sp.	3	0	0.0	0.0
Suborder Sigmurethra				
Family Endodontidae				
Discus cronkhitei	105	0	0.0	0.0
Punctum minutissimum	2	0	0.0	0.0
Family Zonitidae				
Retinella electrina	10	0	0.0	0.0
Euconulus fulvus	131	4	3.0	1.7
Zonitoides arboreus	0	0	0.0	0.0
Vitrina alaskana	19	0	0.0	0.0
Total	605	17	2.4	0.0

[a]Damaged *Vertigo* snails that could not be identified to species.

Table 3. Index of parasite abundance values calculated for all intermediate host species collected on the Sheep River study area in 1984 and 1985.

Snail species	Index of Parasite Abundance 1984	1985
Suborder Orthurethra		
Family Pupillidae		
Vertigo gouldi	0.026	0.039
Vertigo modesta	0.015	0.016
Vertigo spp.[a]	0.010	0
Columella spp.	<0.001	0
Immature pupillids	0.002	0
Suborder Heterurethra		
Family Succineidae		
Catinella sp.	0.003	0.008
Suborder Sigmurethra		
Family Endodontidae		
Discus cronkhitei	0.001	0.004
Family Zonitidae		
Euconulus fulvus	0.037	0.032
Vitrina alaskana	<0.001	0

[a]Damaged *Vertigo* snails that could not be identified to species.

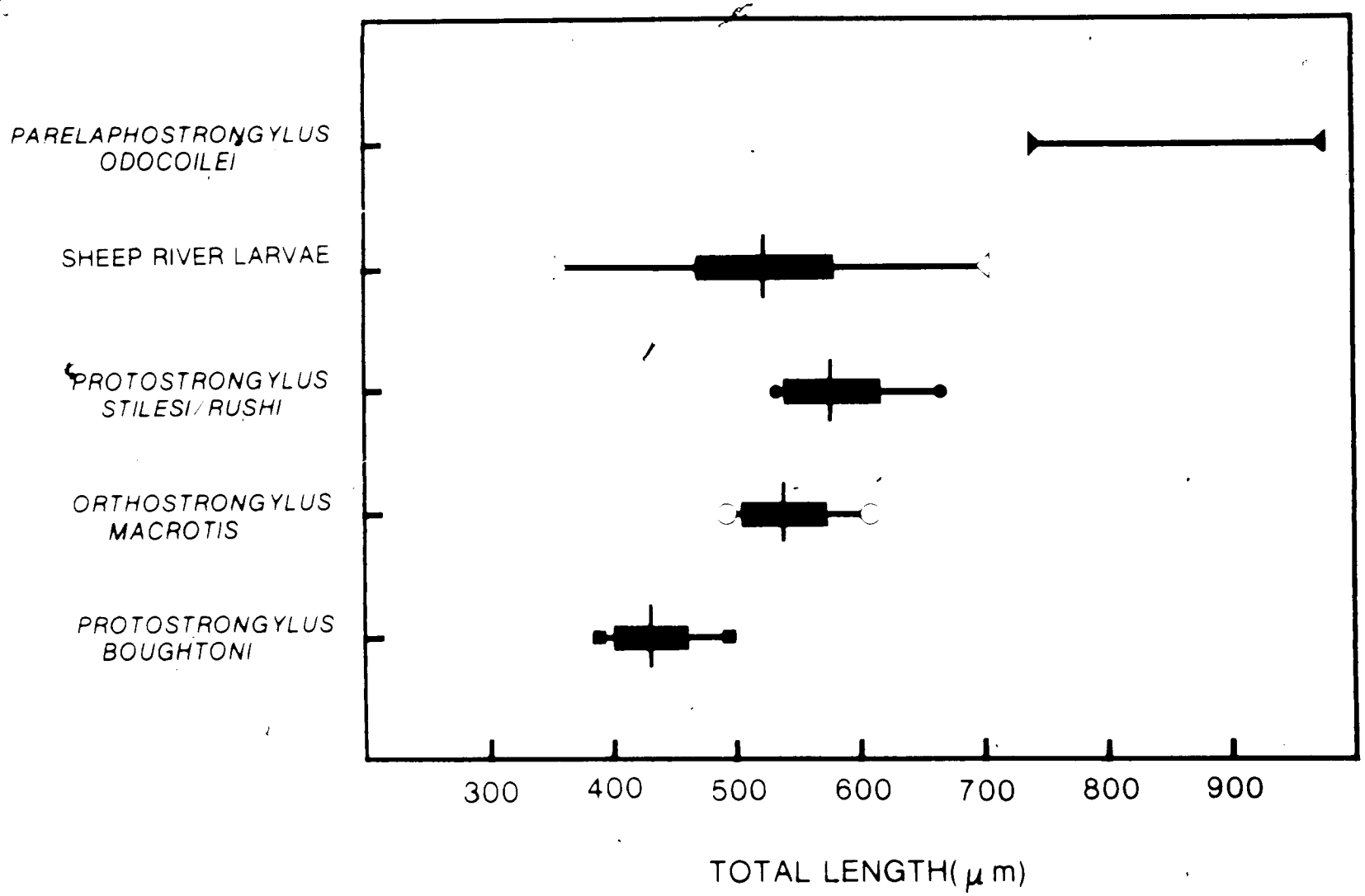
considered the major snail intermediate host species for transmitting lungworm larvae to bighorn sheep. With rare exception (Table 9; p. 64), further analyses of snails were restricted to these species.

Identification of nematode larvae

Total lengths of 113 of the third-stage larvae collected from Sheep River snails were compared to measurements of larvae of known species (Fig. 3). The third-stage larvae exhibited a wide range of total lengths (352 μm - 706 μm), overlapping those of four protostrongylid species, Protostrongylus stilesi/rushi, Orthostrongylus macrotis, and Protostrongylus boughtoni. The mean lengths of the Sheep River larvae did not differ from that of P. stilesi/rushi (t'_s = .820; P > 0.05) or O. macrotis (t'_s = 0.247; P > 0.05). The range of total lengths of third-stage larvae from Sheep River snails did not overlap the range described for Parelaphostrongylus odocoilei, nor did any of the Sheep River larvae possess a 'spine' on the posterior end, a characteristic of P. odocoilei.

Experimental exposure of four mule deer fawns to infective intermediate host snails collected from the Sheep River study area (Appendix I) confirmed the presence of O. macrotis in the snail intermediate host V. modesta.

Figure 3. Third-stage larvae total length measurements of the unidentified Sheep River larvae collected in 1984, compared to those of *Parelaphostrongylus odocoilei* (Ballantyne and Samuel, 1984); *Protostrongylus stilesi/rushi*, *Orthostrongylus macrotis*, and *Protostrongylus boughtoni* (Kralka and Samuel, 1984b).


PARELAPHOSTRONGYLUS ODOCOILEI
SHEEP RIVER LARVAE
PROTOSTRONGYLUS STILESI/RUSHI
ORTHOSTRONGYLUS MACROTIS
PROTOSTRONGYLUS BOUGHTONI
300
400
500
600
700
800
900
TOTAL LENGTH(μm)

Prevalence of *O. macrotis* could not be determined as only one adult worm was recovered.

O. macrotis and *P. stilesi/rushi* third stage larvae were compared using Scanning Electron Microscopy (SEM). Variable tissue damage to the examined larvae made differentiation between *O. macrotis* and *P. stilesi/rushi* third stage larvae difficult. However, neither the number of ridges in the third-stage cuticle, nor the structure of the anterior or tail ends, allowed morphological differentiation between the third-stage larvae of these species.

The distribution of measurements of Sheep River larvae did not differ significantly from a normal distribution (Fig. 4, Kolmogorov-Smirnov test; $P > 0.05$) making it difficult to distinguish different lungworm species. Habitat segregation of lungworm species was not apparent as total length measurements of third-stage larvae did not differ between the four habitat types (Kruskal-Wallis test; $P > 0.05$) (Table 4). Nor was there evidence of lungworm intermediate host specificity as total length measurements of third-stage larvae did not differ between the major intermediate host snail species (Kruskal-Wallis test; $P > 0.05$). As well, there was no correlation between shell diameter of the intermediate host snail species and total length of the third-stage larvae (Spearman rank correlation; $P > 0.05$). Additionally, snails infected with 'short' larvae were often simultaneously infected with 'long' larvae

Figure 4. The distribution of total lengths of the third-stage larvae from infected snails collected at Sheep River in 1984.

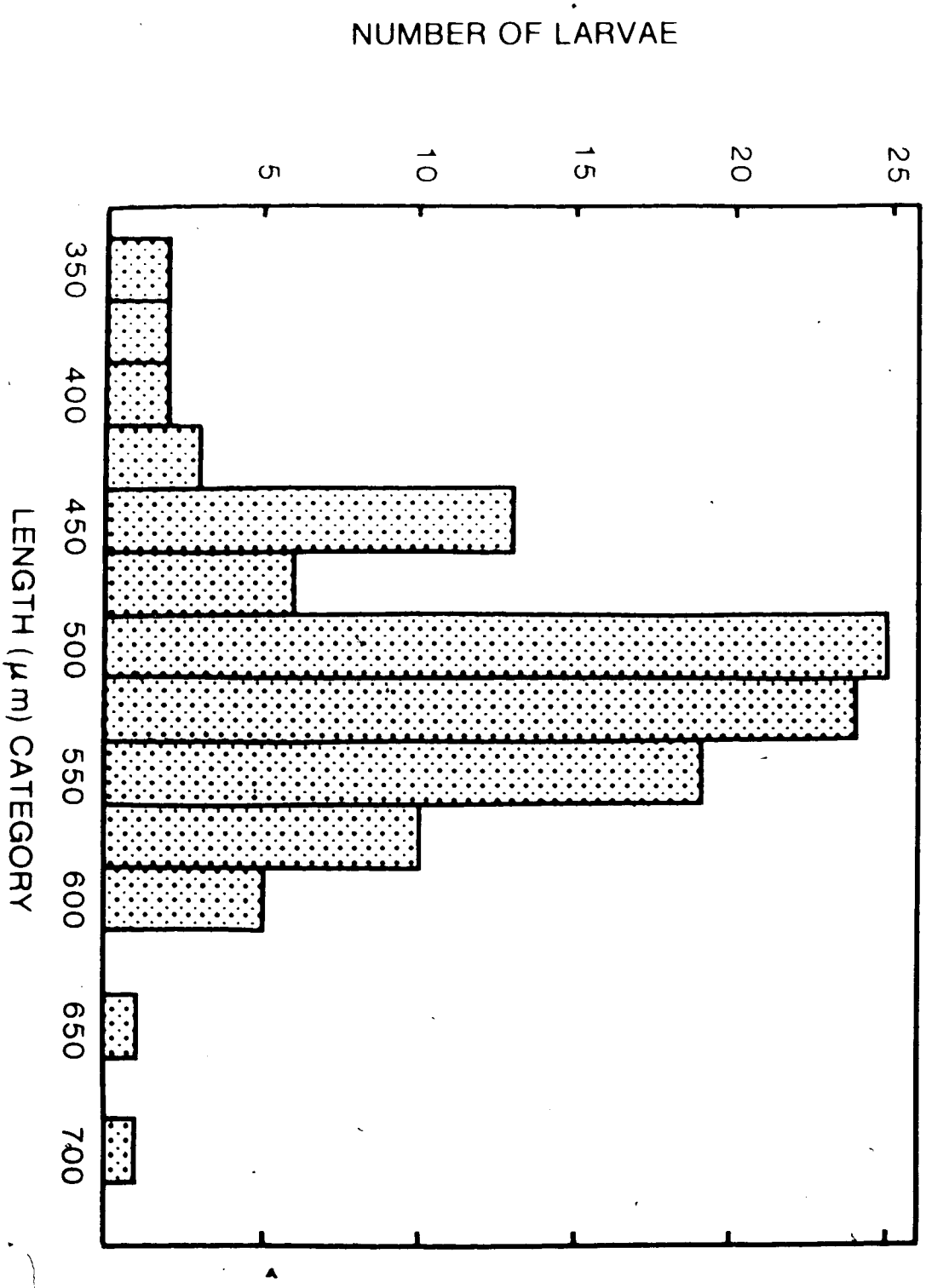

NUMBER OF LARVAE
5
10
15
20
25
LENGTH (μm) CATEGORY
350
400
450
500
550
600
650
700

Table 4. Mean length of protostrongylid third-stage larvae in snails collected in each habitat type in 1984.

Habitat type	n	x̄ length of third-stage larvae (μm)	Standard Deviation
Aspen-center	55	526.49	43.36
Aspen-edge	37	526.17	47.55
Grass-edge	15	534.00	62.38
Grass-center	5	534.80	13.53

(Table 5).

The prevalence of lungworm infection in the major intermediate host snail species was compared between two areas: 1) areas the bighorn sheep herd used frequently; and 2) areas the sheep herd used less frequently. Larvae infecting snails from areas used frequently by sheep were assumed to represent predominantly P. stilesi/rushi; larvae infecting snails from areas used less frequently by sheep were assumed to represent increased numbers of O. macrotis. Prevalence of snail infection did not differ between 'frequent' and 'less frequent' areas ($G = 0.144$; $P > 0.05$). Also, total length measurements of third-stage larvae did not differ between the two areas (Mann-Whitney U-test; $P > 0.05$).

Protostrongylid-type first-stage larvae (likely O. macrotis) were recovered from 88% of the mule deer faecal pellet groups collected from the Sheep River winter range in 1984 and 1985. 'Spined' first-stage larvae were recovered from 94% of the mule deer faecal pellet groups (n = 17); 88% of the pellet groups examined contained concurrent infections of protostrongylid-type and 'spined' larvae. The mule deer at Sheep River were passing mean of 101 larvae per gram wet weight deer faeces (LPG); examination of larvae from faecal samples indicated that approximately 15% were protostrongylid-type. Captive mule deer infected experimentally with O. macrotis shed few first-stage larvae.

Table 5. Total lengths of third-stage protostrongylid type larvae from infected snails with multiple infections.

Snail Species	Total length of L3 (μm)
Euconulus	558 392
	468 574
	520 518 566 592
	510 530
	550 576 578 530 546
	474 486 462
	508 534 516 548 554 534 494 508 460 486 510
	486 504 554 448 510
	410 520
Vertigo gouldi	510 548
	554 520 592 518
	610 570
	546 556 520
	544 538 464 556
	468 530
Vertigo modesta	588 540
	550 512 540
	706 540 664 580
	450 441
Vertigo spp.	474 514 528
Catinella spp.	540 524

For example, a mule deer infected with 199 L3 O. macrotis shed a mean of 5 LPG over a 3 month period, while a second deer infected with 200 L3s shed a mean of 2.5 LPG over 1.5 months (Samuel, unpublished data). As well, a wild mule deer captured as a yearling had a natural infection of O. macrotis and shed a mean of 50.6 LPG over a 1.5 month period (Samuel, unpublished data). Although the prevalence of protostrongylid type larvae is high in the mule deer faecal samples collected from Sheep River, the production of first stage larvae may be relatively low when compared to the $\bar{x}$ LPG $\simeq$ 465 from bighorn sheep (Festa-Bianchet, pers. comm., 1987).

Although the presence of O. macrotis is confirmed, evidence presented here suggests that many of the larvae infecting the snails on the winter range are those of P. stilesi/rushi. In addition, numerous bighorn sheep (approximately 160 individuals) were concentrated on the study area from September to May when their faecal larval 'output' was high ($\bar{x}$ LPG $\simeq$ 465; Festa-Bianchet, 1987) while, mule deer were few in number and their faecal larval 'output' was low.

Timing of Transmission

The prevalence (number of E. fulvus, V. gouldi, V.

modesta infected/number of same examined) of intermediate hosts infected with third-stage (infective) larvae differed by month on sheep winter range (G = 24.64; P < .001) (Fig. 5). Relative to other studies, prevalence of infective snails was high during all months. Prevalence of infective snails was highest during September, 1984 and April, 1985, overlapping the time when bighorn sheep were present on the winter range (Figs. 5,6).

The prevalence of infection did not differ between September 1984 and April 1985, providing no evidence for significant overwinter mortality of infected snails (G = 0.717, P > 0.05). The proportion of infective (L3) and noninfective (L2 and/or L1) larvae infecting snail intermediate hosts differed by season (G = 8.644, P < 0.025)(Fig. 7).

Prevalence of infection differed significantly between size classes of *E. fulvus* (G = 17.84; P < 0.005). There was a positive correlation between size and prevalence of infection (Fig. 8). The infected snails collected in all seasons were generally adult stages (Table 6). Monthly size class distributions of *E. fulvus* indicated that juvenile stages were most abundant during May and June, 1984, and April and May, 1985. Juvenile recruitment was not

Figure 5. Monthly prevalence of infective Euconulus fulvus, Vertigo gouldi, and Vertigo modesta intermediate host snails, calculated from 1984 and 1985 permanent plot data.

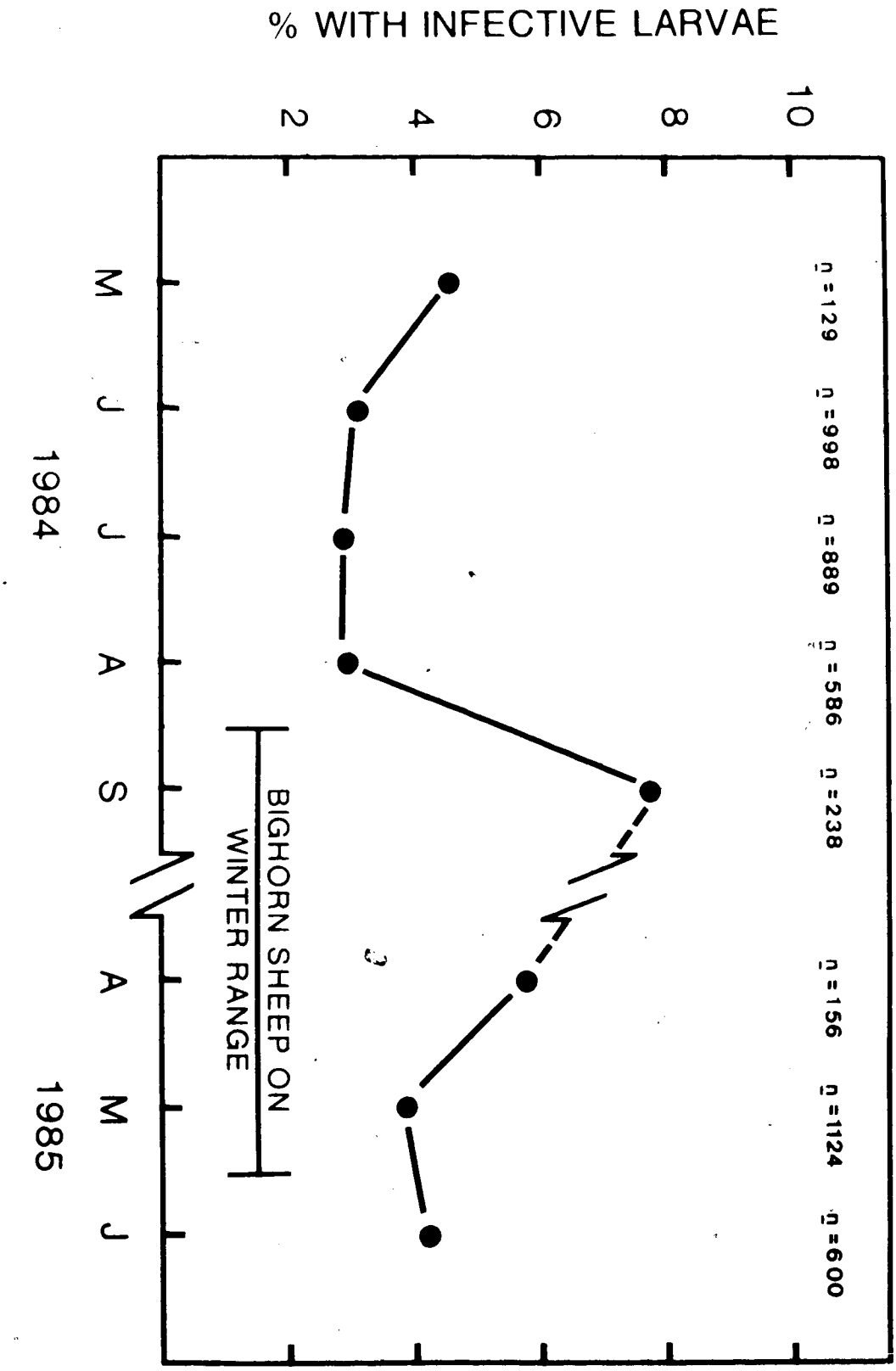

% WITH INFECTIVE LARVAE
2
4
6
8
10
n=129
n=998
n=889
n=586
n=238
n=156
n=1124
n=600
BIGHORN SHEEP ON WINTER RANGE
M
J
J
A
S
A
M
J
1984
1985

Figure 6. Monthly prevalence of infective Euconulus fulvus, Vertigo gouldi, and Vertigo modesta intermediate host snails calculated from 1984 litter sample data.

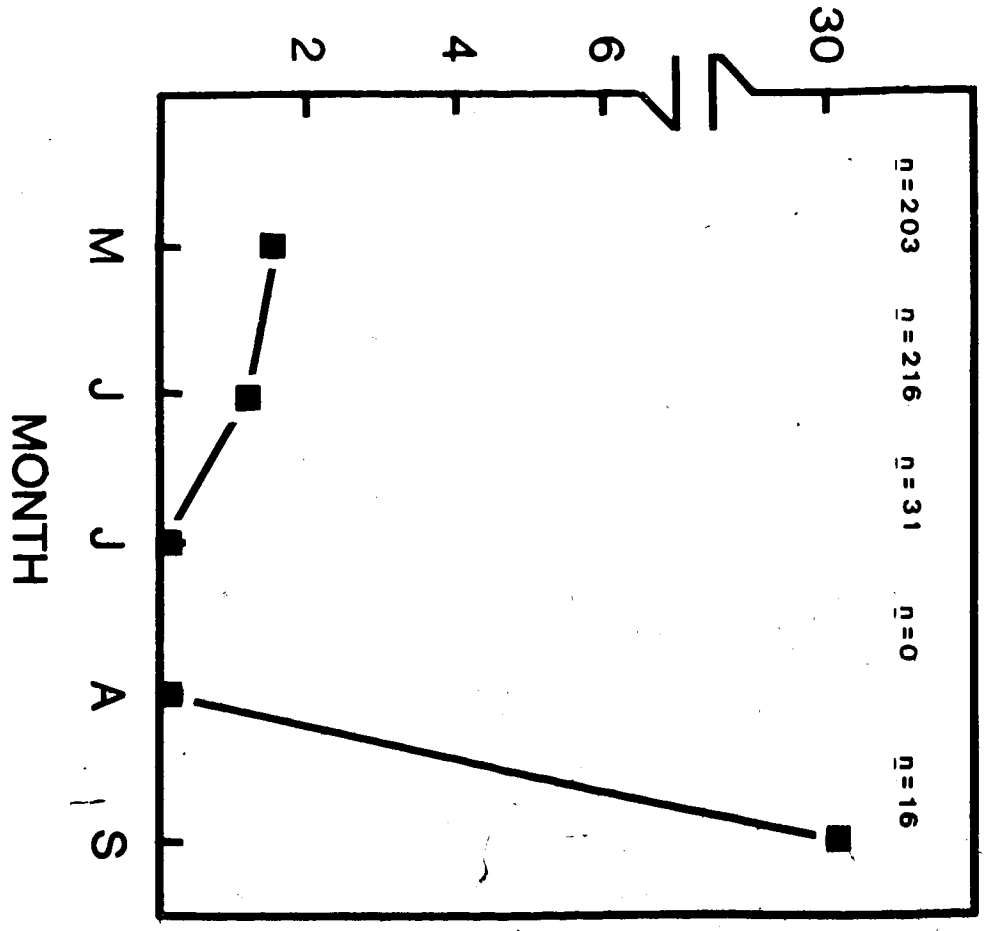
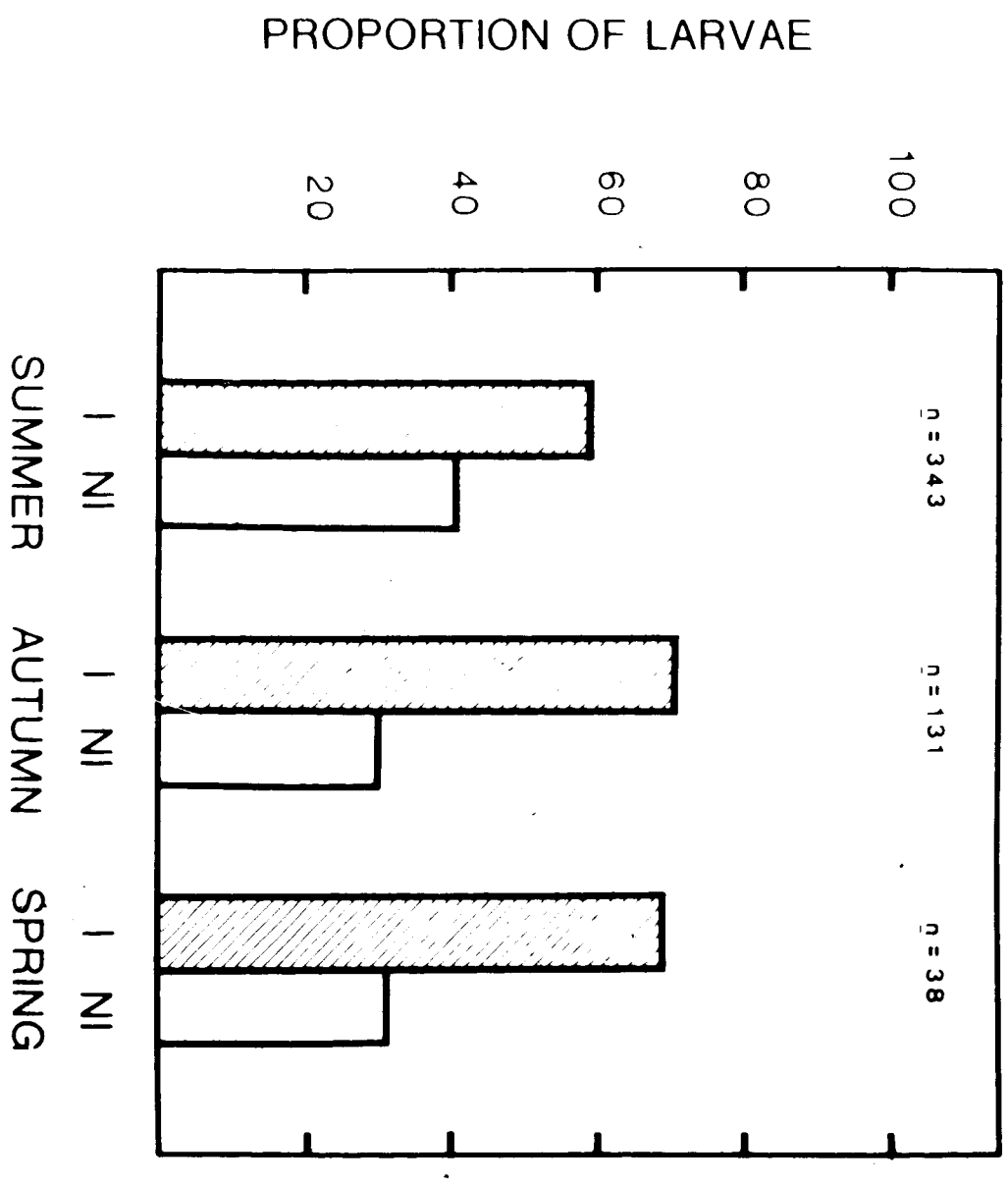

% WITH INFECTIVE LARVAE
2
4
6
30
MONTH
M
J
J
A
S
n=203
n=216
n=31
n=0
n=16

Figure 7. The proportion of infective (I), and noninfective (NI) larvae infecting snail hosts on a seasonal basis for summer, 1984; autumn, 1985; and spring 1985 (from permanent plot data).


PROPORTION OF LARVAE
20
40
60
80
100
n = 343
n = 131
n = 38
SUMMER
AUTUMN
SPRING
I NI
I NI
I NI

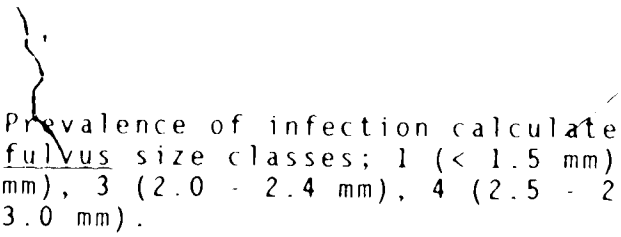


Figure 8. Prevalence of infection calculated for Euconulus fulvus size classes; 1 (< 1.5 mm), 2 (1.5 - 1.9 mm), 3 (2.0 - 2.4 mm), 4 (2.5 - 2.9 mm), 5 (≥ 3.0 mm).

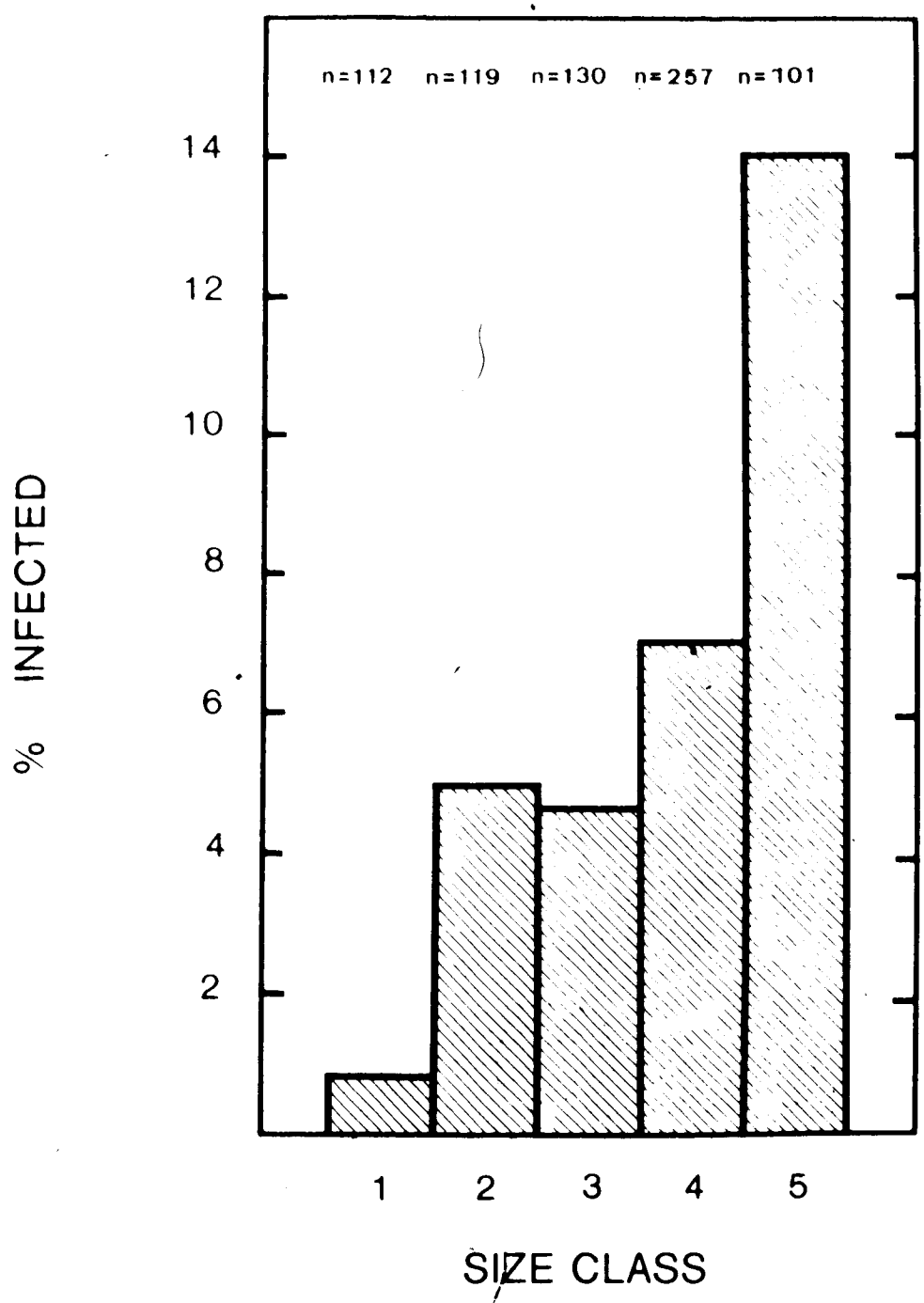

n=112 n=119 n=130 n=257 n=101
14
12
10
8
6
4
2
% INFECTED
1 2 3 4 5
SIZE CLASS

Table 6. Proportion of adult, and juvenile, infected snails collected during summer, 1984, autumn, 1984, and spring, 1985.

Season	n	% Adult	% Juvenile
Summer	113	90.3	9.7
Autumn	28	82.1	17.9
Spring	16	81.2	18.8

accompanied by a noticeable die-off of large, older snails (Fig. 9). No correlation was found between intensity of infection (calculated from presence of second and third-stage larvae) and shell size for E. fulvus (n = 53, r^2 = 0.128; P = 0.353)(Fig. 10).

Snail density in litter samples in 1984 was highest during May, declined during the months of July and August, and increased to the July level in September (Table 7). Snail density was highest in aspen-edge, and aspen-center sites during summer but in grass-edge and aspen-edge sites during autumn (Table 8). An analysis of dispersion (variance/mean x number of samples) indicated that snails had clumped distributions in all habitat types (Table 8).

The density of snails collected from litter samples in 1984 was correlated with the weekly precipitation level (r^2 = 0.589; P = 0.002) (Fig. 11), snail density increased with increased precipitation. A similar trend was observed for the mean weekly number of intermediate host snails/permanent plot and weekly precipitation (r^2 = 0.259; P = 0.076). Temperature did not influence the mean weekly number of intermediate host snails/permanent plot (r^2 = 0.009; P = 0.747). However, a multiple regression of mean weekly number of intermediate host snails/board, on weekly precipitation and mean weekly temperature, suggested that the number of snails/board was influenced by both precipitation and temperature (Snails/board = -2.046 + 0.098

Figure 9. Monthly size class distributions of *Euconulus fulvus* snails; 1 (< 1.5 mm), 2 (1.5 - 1.9 mm), 3 (2.0 - 2.4 mm), 4 (2.5 - 2.9 mm), 5 (≥ 3.0 mm).

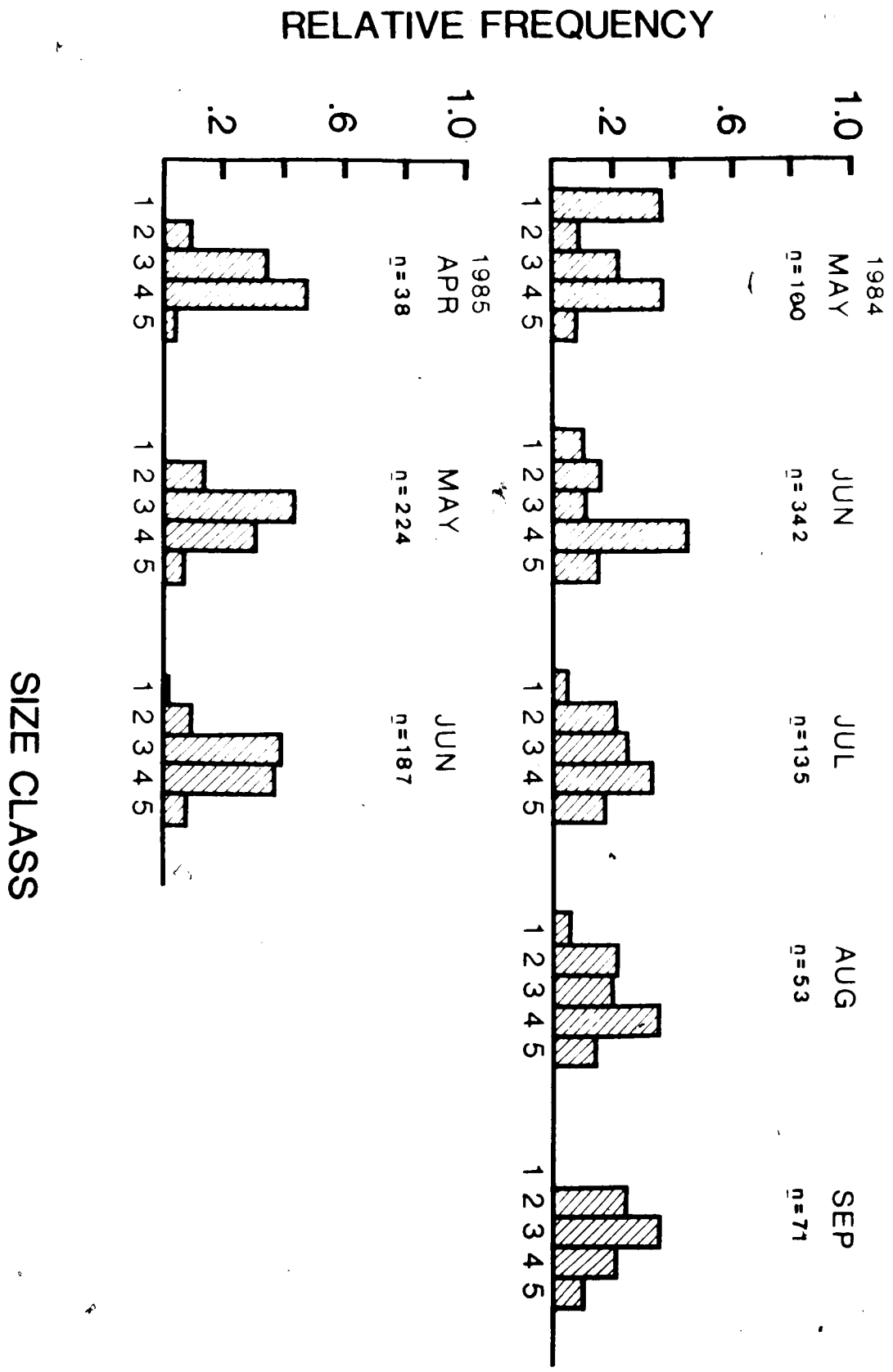

RELATIVE FREQUENCY
1.0
.6
.2
1984
MAY
n=100
JUN
n=342
JUL
n=135
AUG
n=53
SEP
n=71
1985
APR
n=38
MAY
n=224
JUN
n=187
1 2 3 4 5
SIZE CLASS

Figure 10. Intensity of protostrongylid infection compared to shell size of Euconulus fulvus snails.

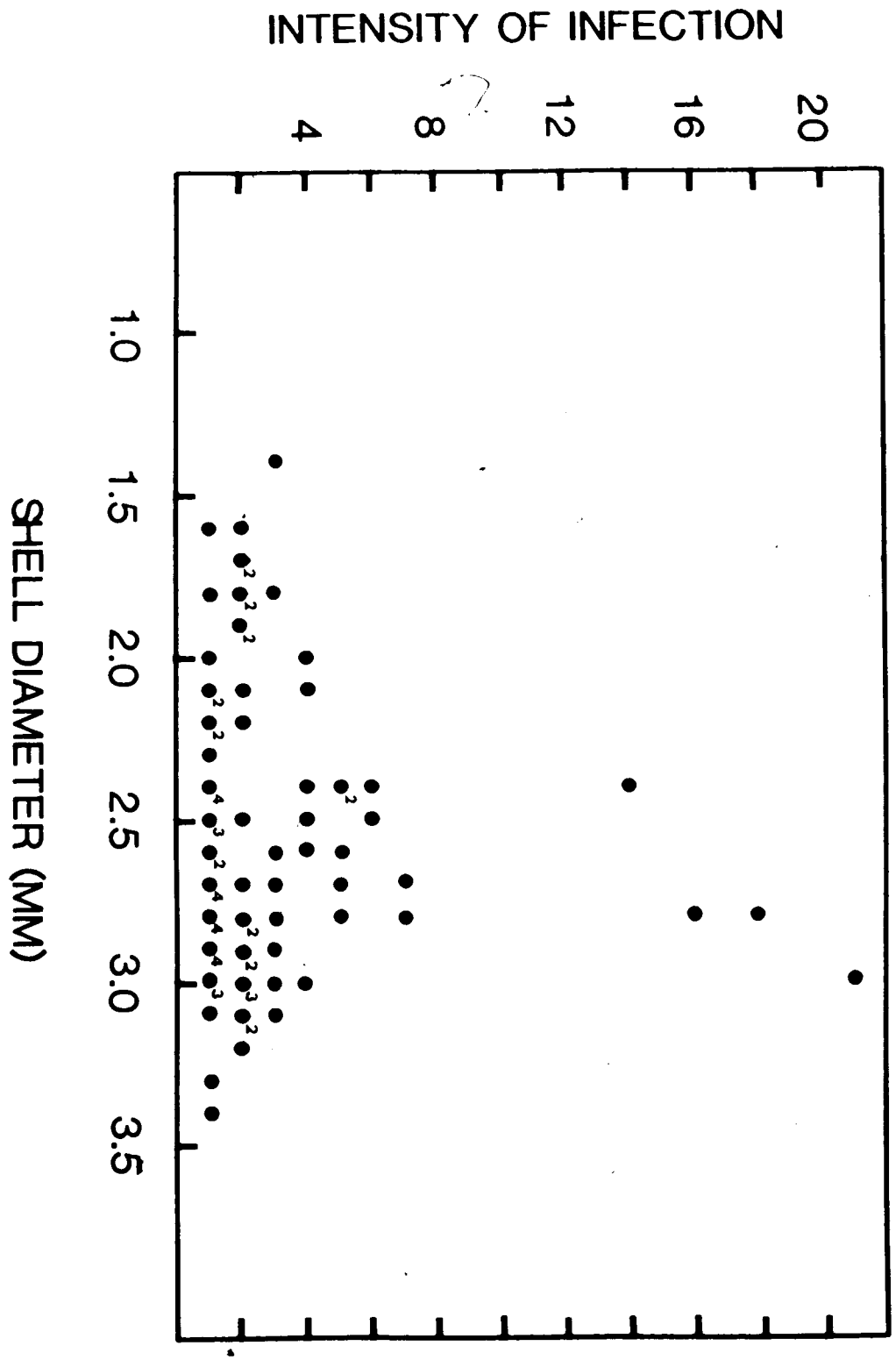

INTENSITY OF INFECTION
4
8
12
16
20
1.0
1.5
2.0
2.5
3.0
3.5
SHELL DIAMETER (MM)

Table 7. Monthly snail density (number/m^2) of Euconulus fulvus, Vertigo gouldi, and Vertigo modesta intermediate host species from litter samples collected in 1984 on the Sheep River study area.

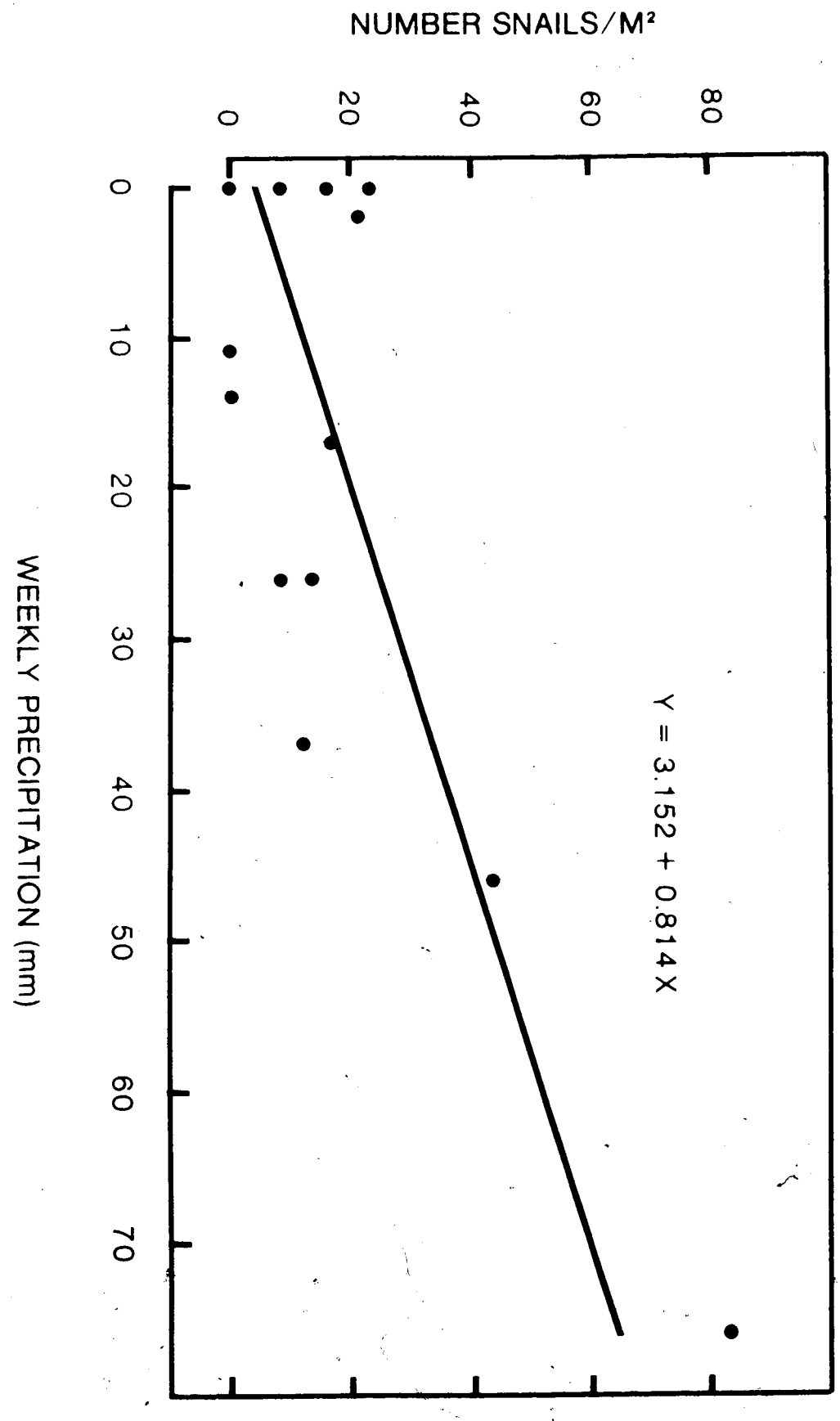
Month	Number of Samples	Density	Standard Deviation
May	120	38.5	119.05
June	120	34.16	87.06
July	96	12.08	23.03
August	72	0	0
September	24	13.33	31.57

Table 8. Mean snail density (number/m^2) of Euconulus fulvus, Vertigo gouldi, and Vertigo modesta in each habitat type during summer and autumn 1984 on the Sheep River study area.

Habitat type	Number of samples	$\bar{x}$ (SD)	Coefficient[a] of dispersion
Summer			
Aspen-Center	78	21.53 (42.61)	329.07[b]
Aspen-Edge	78	27.19 (71.20)	727.00[b]
Grass-Edge	78	3.07 (10.23)	132.69[b]
Grass-Center	78	0.77 (5.04)	128.79[b]
Autumn			
Aspen-Center	15	1.33 (5.16)	15.04
Aspen-Edge	15	9.33 (26.04)	54.56[b]
Grass-Edge	15	10.66 (31.90)	71.77[b]
Grass-Center	15	0.0	0.0

[a]Coefficient of dispersion = $(s^2n)/\bar{x}$.
[b]$p < 0.001$.

Figure 11. Regression of snail density (number/m^2) on mean weekly precipitation level for summer 1984.


NUMBER SNAILS/M²
0
20
40
60
80
WEEKLY PRECIPITATION (mm)
0
10
20
30
40
50
60
70
Y = 3.152 + 0.814 X

(temperature) + 0.022 (precipitation); r^2 = 0.501; P = 0.030).

Location of transmission

Infective snails and noninfective snails collected from the permanent plots were most numerous in the aspen center and aspen edge habitats during all seasonal periods (Fig. 12). The proportion of infective snails did not differ between the four designated habitat types for summer 1984 (G = 5.333; $P > 0.05$), autumn 1984 (G = 4.669; $P > 0.05$), or spring 1985 (G = 3.322; $P > 0.05$). However, when data for these periods were combined, a relatively higher proportion of the snails in grass-edge and grass-center areas were infective than in the aspen-center or aspen-edge areas (Fig. 13).

Bighorn sheep were observed in the edge and center of aspen and grass habitats during all observation times (Fig. 14). Because sheep are easier to observe in open habitat than treed habitat, observations of bighorn sheep in aspen edge and center areas are probably conservative, some sheep not observed during observation times were probably in aspen areas.

A total of 683 sheep sightings were in aspen-edge and aspen-center areas, 10.8% of the total 6298 sheep sightings.

Figure 12. Proportion of infective (I) and noninfective (NI) snails collected from permanent plots in the four habitat types at Sheep River, Alberta.

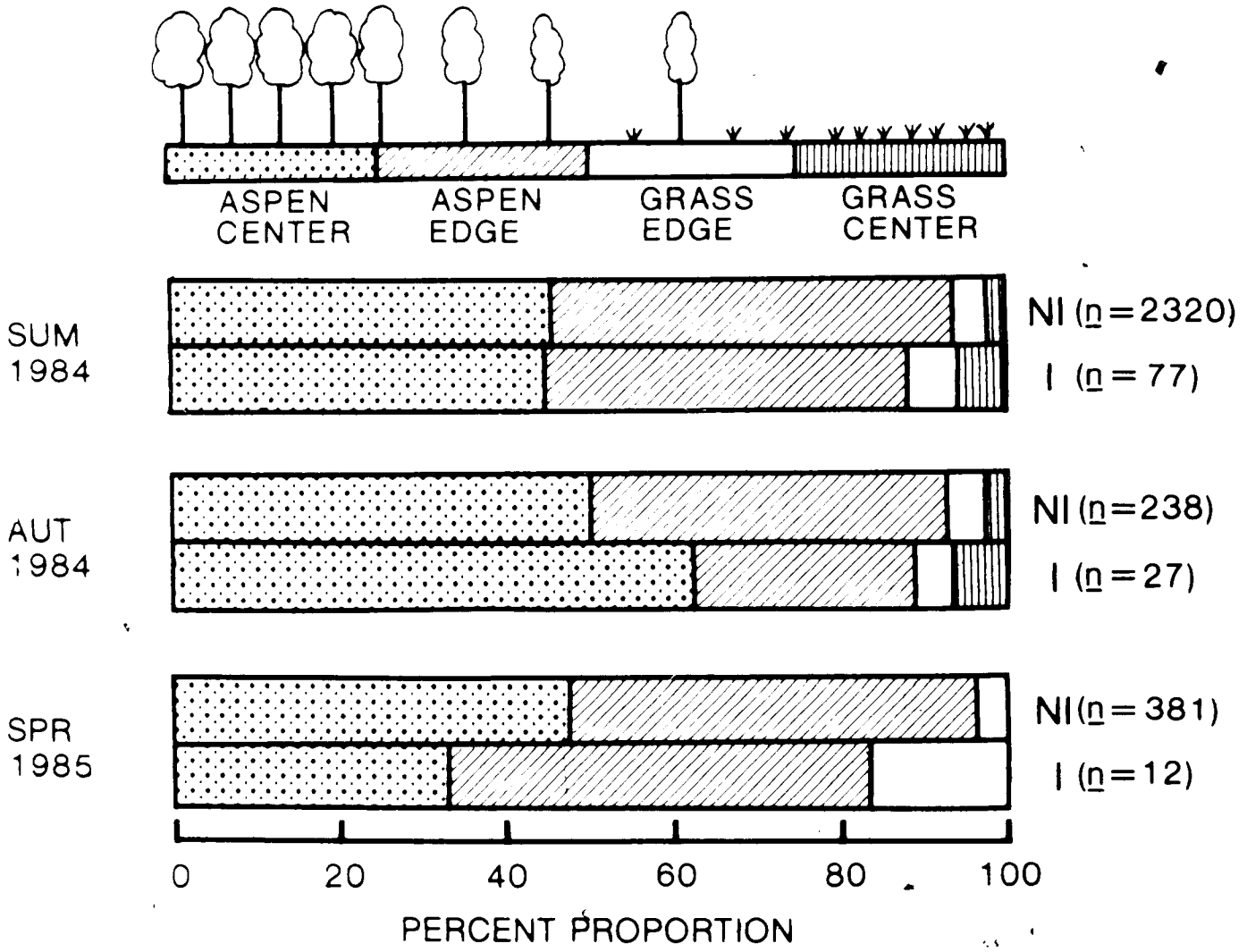

ASPEN CENTER
ASPEN EDGE
GRASS EDGE
GRASS CENTER
SUM 1984
NI (n=2320)
I (n=77)
AUT 1984
NI (n=238)
I (n=27)
SPR 1985
NI (n=381)
I (n=12)
0
20
40
60
80
100
PERCENT PROPORTION

Figure 13. Proportion of infective (I) and noninfective (NI) snails in the four habitat types, data for all seasons (summer, 1984; autumn, 1985; and spring, 1985) were combined.

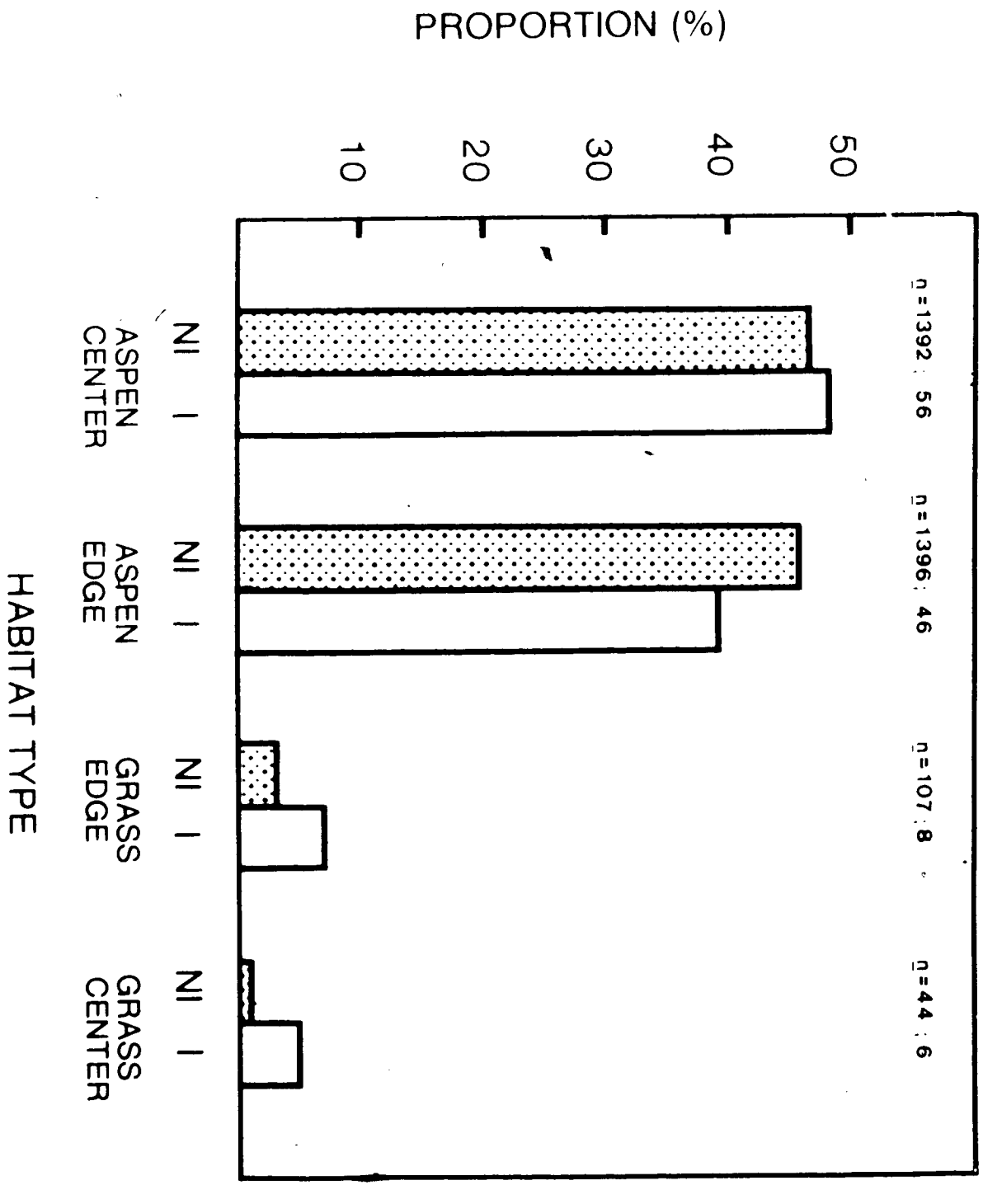
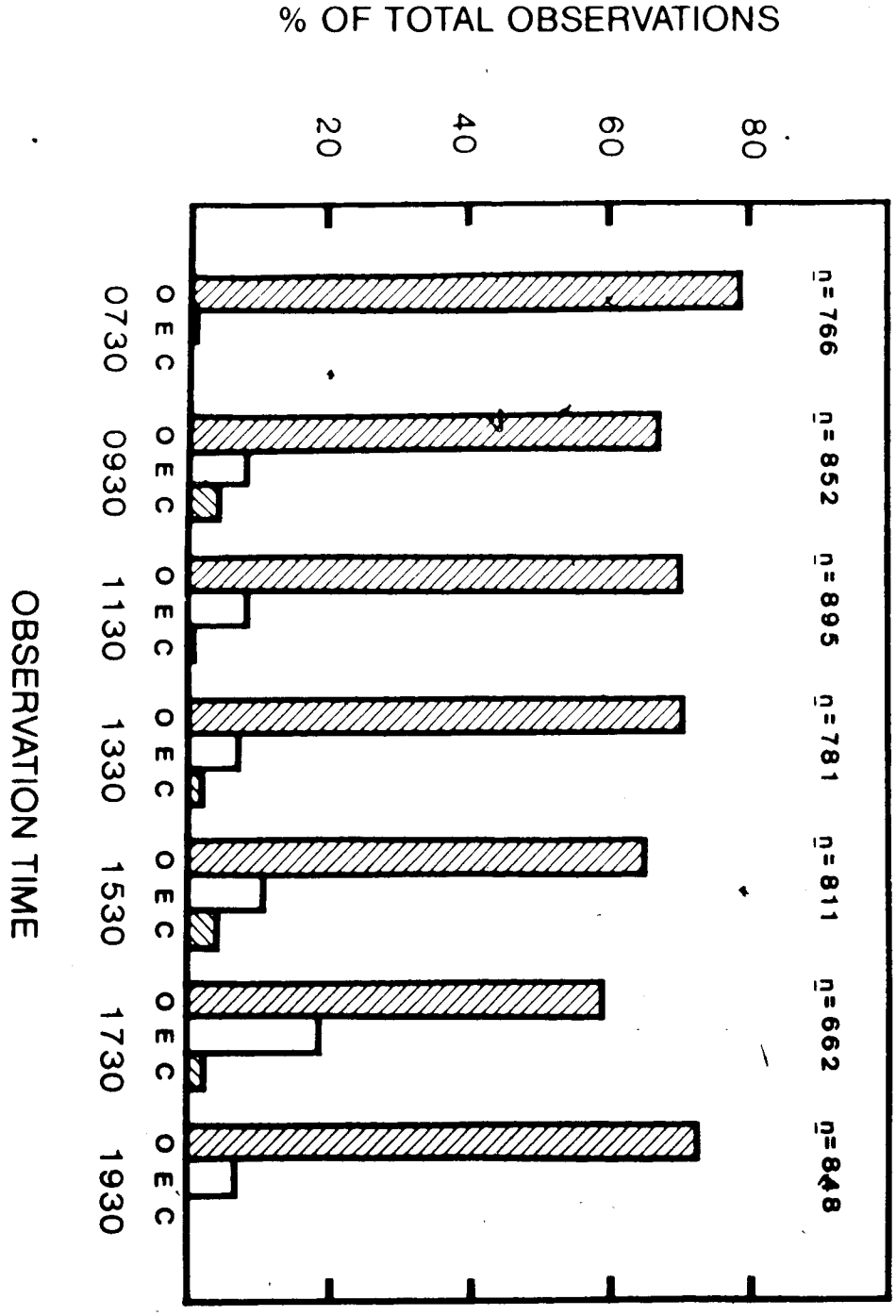

PROPORTION (%)
10
20
30
40
50
n=1392 : 56
n=1396 : 46
n=107 : 8
n=44 : 6
NI
ASPEN CENTER
NI
ASPEN EDGE
NI
GRASS EDGE
NI
GRASS CENTER
HABITAT TYPE

Figure 14. Proportion of bighorn sheep sightings in aspen/grass-edge, aspen-center, and grass-center areas for all observation times.


% OF TOTAL OBSERVATIONS
20
40
60
80
n̄= 766
n̄= 852
n̄= 895
n̄= 781
n̄= 811
n̄= 662
n̄= 848
O E C
0730
0930
1130
1330
1530
1730
1930
OBSERVATION TIME

Sheep were observed feeding during 80.2% of the sighting recorded in aspen-edge and aspen center areas. Sheep were observed eating the vegetative heads of tall vegetation (grasses), and unknown forage parts close to the ground in short vegetation.

An index of lungworm availability to bighorn sheep, (prevalence x intensity x density), was calculated for the aspen-center, aspen-edge, grass-edge, grass-center habitats for spring, summer and autumn, 1984 (Table 9). During spring and summer 1984, index values were highest in the aspen-center and aspen-edge habitats; index values were highest in aspen-edge and grass-edge habitats during autumn.

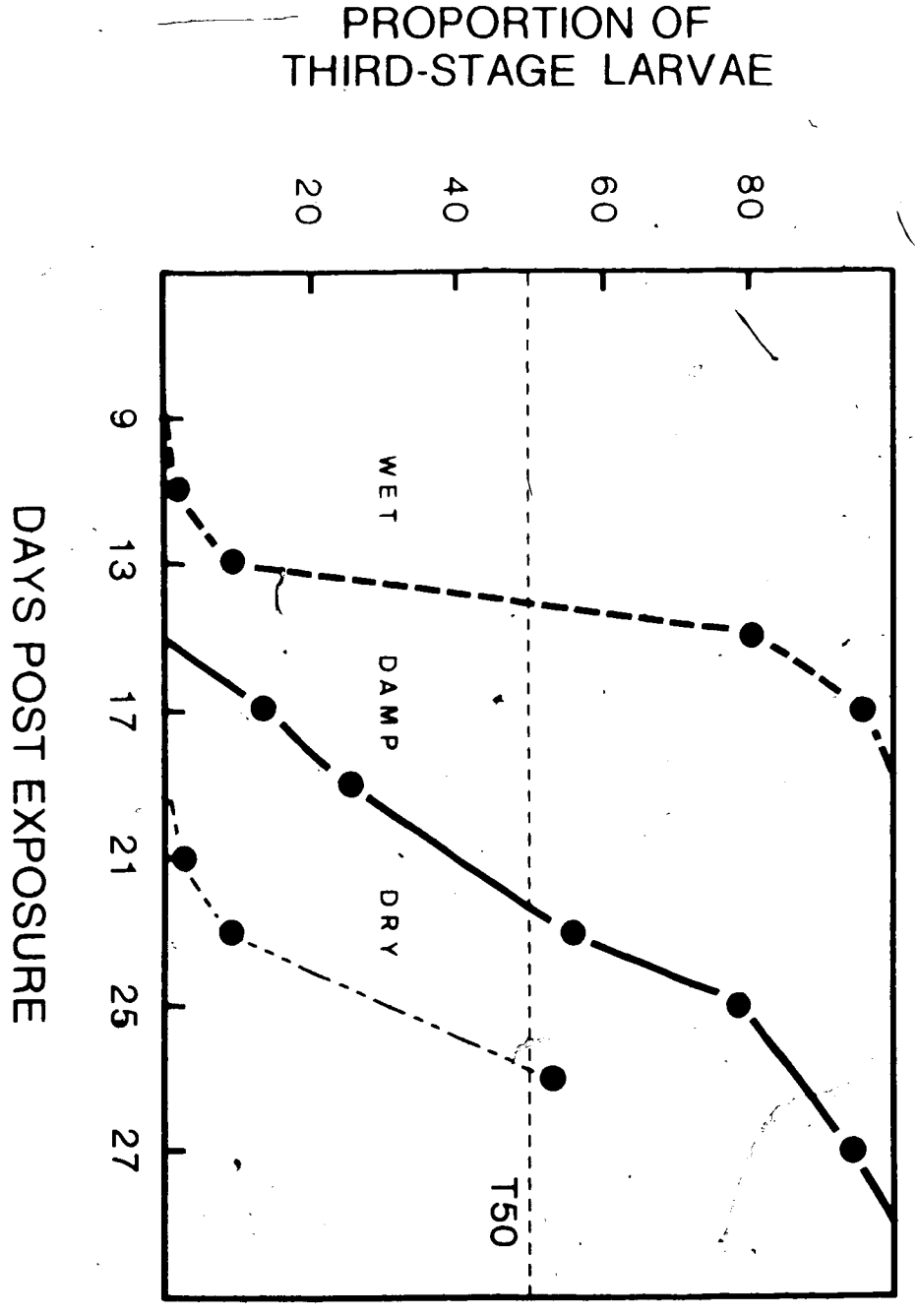
The effect of moisture on Protostrongylus stilesi/rushi development

The rate of larval development varied among the three moisture regimes (Fig. 15). Third-stage larvae were first observed 11, 17, and 21 days post-exposure in snails in wet damp and dry conditions, respectively. The time when 50% of the experimental snails were observed infected with third-stage larvae (T50) was 14, 22, and 27 days post-exposure in snails kept in wet, damp, and dry conditions respectively. The number of development days from initial observation of larvae in the feet of snails to T50 did not differ greatly

Table 9. Index of parasite availability values (prevalence of infective snails x intensity x density) calculated for the major intermediate hosts in each habitat during spring, summer, and autumn, 1984.

Season	Habitat Type: Aspen Center	Aspen Edge	Grass Edge	Grass Center	Sum
Spring					
Prevalence	0.012	0.013	0	1.000	
Intensity	1.000	1.000	0	2.000	
Density	112.000	102.600	4.0	1.2	
Product	1.344	1.333	0	2.400	5.077
Summer					
Prevalence	0.030	0.030	0.058	0.135	
Intensity	2.600	2.085	2.800	2.600	
Density	22.307	27.179	3.146	1.138	
Product	1.739	1.700	0.511	0.399	4.349
Autumn					
Prevalence	0.121	0.066	0.077	0.600	
Intensity	3.235	1.571	1.000	2.000	
Density	1.333	9.333	10.666	0	
Product	0.523	0.967	0.821	0	2.311

Figure 15. Rates of development of *Protostrongylus stilesi/rushi* larvae in snails housed at three moisture regimes; wet, damp, and dry.


PROPORTION OF
THIRD-STAGE LARVAE
20
40
60
80
9
13
17
21
25
27
DAYS POST EXPOSURE
WET
DAMP
DRY
T50

between snails in the three moisture regimes: 3 days for wet; 5 days for damp; and 6 days for dry.

Unfortunately the total lengths of the third-stage larvae reared in the experimental snails were not measured.

DISCUSSION

Identification of nematode larvae

The range of total lengths of third-stage larvae overlapped the range of measurements described for Protostrongylus stilesi/rushi, Orthostrongylus macrotis, and Protostrongylus boughtoni (see Kralka and Samuel, 1984b). This wide range of measurements suggests that 1) the snail intermediate hosts are infected with different species of protostrongylid lungworms or 2) larvae from snails collected in the field are more variable in length than those reared in laboratory snails. The mean length of the larvae did not differ from that of P. stilesi/rushi or O. macrotis, suggesting that both of these species may infect the snails at Sheep River. The distribution of the larvae measurements did not differ from a normal distribution, making it difficult to distinguish different lungworm species. Habitat segregation between different lungworm species was not detected for total length measurements of larvae from aspen-center, aspen-edge, grass-edge, and grass-center areas.

Snowshoe hares in Alberta can be infected with P. boughtoni (Kralka and Samuel, 1984a). However, hares, their tracks or pellets, were not observed on the study area (personal observation; Festa-Bianchet pers. comm., 1985).

If hares were present, they were not in high numbers, and as a result, few, if any, of the parasites on the study area are likely to be P. boughtoni.

The presence of O. macrotis in the infected snails on the winter range, as determined by successful experimental passage to mule deer (Appendix I), made it necessary to determine whether or not P. stilesi/rushi and O. macrotis larvae could be differentiated. Total lengths of third-stage larvae (Kralka and Samuel, 1984b), and SEM morphological examination, failed to distinguish between known specimens of P. stilesi/rushi and O. macrotis third-stage larvae. Kralka and Samuel (1984b) stated, "specific structural differences may be found among Protostrongylus and Orthostrongylus infective larvae", and they suggested that a good starting point would be to remove the first-stage cuticle. However, "removal of this cuticle without damaging the larva inside, though not impossible, is extremely difficult and time-consuming".

There is, nonetheless, circumstantial evidence that P. stilesi/rushi commonly infect snail intermediate hosts on the study area. For instance, all snails were collected from an area predictably used from September to May by a herd of approximately 160 bighorn sheep. Late winter months, when sheep are on the winter range, are also the peak time of first-stage protostrongylid larvae production in bighorn sheep (Uhazy et al., 1973). Faecal analysis of

sheep pellets from the Sheep River herd indicated that all individuals were likely infected with lungworm, counts of mean LPG = 466 were recorded in 1984, and mean LPG = 461 in 1985 (Festa Bianchet pers. comm., 1987). Additionally, mule deer density on the study area was relatively low (personal observation), as was intensity of larvae in faeces, compared to that of bighorn sheep.

Festa Bianchet (1982) recorded bighorn sheep feeding patterns on the study area, and observed 26% of sheep sightings in aspen areas during September - October, and 25% in aspen copses during December - May. Sheep using aspen copses on the winter range would 'seed' these areas with first-stage P. stilesi/rushi larvae; aspen copses on the winter range are also favourable habitats for snail populations (Boag and Wishart, 1982).

The presence of O. macrotis is an inherent problem when examining the infected snails from the bighorn sheep winter range at Sheep River. Identification of different protostrongylid species based on total length measurements of the third-stage larvae is difficult given the considerable overlap between larvae measurements of known species, and the variability of the larvae measurements from Sheep River. Additionally, snails were infected with larvae of variable size; thus, snails could not be eliminated from analyses based on the lengths of their third-stage larvae.

Although P. stilesi/rushi larvae could not be

identified in snails from the winter range, the overlap of third-stage larvae measurements from Sheep River with that recorded for P. stilesi/rushi, the high density of bighorn sheep, their high faecal larval output, and their use of aspen copses, suggests that many of the third stage larvae infecting snail intermediate hosts on the study area are P. stilesi/rushi.

The range of third-stage protostrongylid larvae measurements from Sheep River is considerably wider than previously recorded for P. stilesi/rushi and Q. macrotis third-stage larvae. It is possible that inconsistent developmental conditions affected the total length of Sheep River larvae. Kralka and Samuel (1984b) examined total lengths of third-stage larvae reared in laboratory infected snails. Despite standardization of development conditions, they recorded a considerable range in lengths of third stage larvae for each protostrongylid species examined. If there is this much variability in lengths of third-stage larvae under standardized conditions, then it should not be surprizing that there was a wide range of measurements for Sheep River larvae which developed in uncontrolled diverse conditions. These diverse conditions included variable temperature and humidity and the fact that larvae were collected from seven snail species, the snails being of different ages.

Stanislawski and Becker (1979) suggested that reduced

blood glucose levels in snails infected with Schistosoma mansoni (Trematoda:Schistosomatidae) might be attributed to use of host metabolites by larvae. Svarc and Zmoray (1974) concluded that sole glands in the foot of the snail species Cepaea vindobonensis and Succinea putris acted as 'nutrition donors' for developing Muellerius tenuispiculatus larvae. As well, Skorping (1984) found development rates of Elaphostrongylus rangiferi (Nematoda:Metastrongyloidea) larvae reared in starved snails were significantly slower than those of larvae reared in fed snails. Snail host 'starvation' might similarly affect the rate of R. stilesi/rushi larval development.

Ambient temperatures during the summer months are optimum for rapid larval development (Samson and Holmes, 1985). Summer months are also when some terrestrial snail species are periodically inactive, and estivate (Newell and Appleton, 1979). The trend of decreased number of snails/permanent plot with decreased precipitation, suggests that activity of the intermediate host snails at Sheep River is affected by environmental conditions, during unfavourable conditions these snails may be inactive. At the least, they were difficult to collect. What effect snail 'starvation' during estivation and/or inactivity has on larval development is unclear. Lankester and Anderson (1968) reported slower development of Pneumostrongylus tenuis (= Parelaphostrongylus tenuis) in estivating snails, Mesodon

thyroidus, than in nonestivating snails. If larvae are nutritionally dependent on the snail host, estivation or hibernation induced starvation of the snail host may create unfavourable and/or stressful conditions for larval development, and possibly, infected snails estivating for long and/or frequent periods might have smaller larvae than infected snails living in more favourable microhabitats.

The infected snails from Sheep River are exposed to a large population of first-stage larvae while laboratory infected snails are generally exposed to the first stage larvae from only a few bighorn sheep. Thus, variability in the total lengths of P. stilesi/rushi may be greater in the 'field' larvae than the 'laboratory' larvae.

Timing of transmission

Gastropod transmission of P. stilesi/rushi to bighorn sheep is likely to occur during periods when sheep and infective snails are active, abundant, and have overlapping distributions. At Sheep River, the prevalence of infective snails was high during all months but was highest during September and October, when bighorn sheep were on the winter range, lending support to the Boag/Wishart hypothesis of an autumn period of lungworm transmission. However, the prevalence of infective snails was also high during April

1985, suggesting that spring is also a favourable time for transmission because bighorn sheep remain on the winter range until mid-May.

Selective overwinter mortality of infected snails would have emphasized autumn as the major time for lungworm transmission to bighorn sheep. However, significant overwinter mortality of infected snails was not detected in this study. Literature on this subject is contradictory. Skorping (1985) showed that fecundity of Arianta arbustorum snails infected with E. rangiferi was lower than fecundity of uninfected snails. Mortality of juvenile A. arbustorum increased with increasing intensity of infection (Skorping, 1985). However, Samson (1984) conducted laboratory experiments using the snail host Vallonia pulchella, and found no difference in fecundity, mortality, or growth rate between uninfected individuals and those infected with P. stilesi/rushi. The lack of detected over-winter mortality of the infected snails at Sheep River, coupled with Samson's (1984) findings, suggests that snails infected with P. stilesi/rushi may not be affected adversely.

Boag and Wishart (1982) proposed that increased snail density in late summer and early autumn would promote transmission of lungworms to bighorn sheep because infected snails would be most available at this time. If juvenile snails were becoming infected during the summer, and comprised the infected snail population during autumn, most

of the infective snails collected during autumn should have been juvenile or early adult stages. This was not the case. Infective snails collected during autumn were predominantly large adult snails. If juvenile snails were responsible for the increased frequency of infected snails noted in autumn, juveniles infected with second-stage larvae should have been prevalent during summer. This was not observed. Infected snails collected during summer were, generally, large snails. Although potentially differing habitat requirements between juvenile and adult snails may have made it difficult to detect infected juvenile stages during summer, these stages should have been collected during autumn.

An increased number of snails/permanent plot was noted during August, 1984 supporting observations of Boag and Wishart (1982). However, snails were not collected from litter samples during August, suggesting that snails were highly aggregated during late summer. The increased number of snails/permanent plot during August, 1984 may reflect snail activity. For instance, 76% of the snails collected by permanent plot sampling were collected on August 3rd. All but the later part of July was dry, suggesting that the large number of snails collected on 3 August was influenced by precipitation during the end of July and beginning of August (including 3 August). Additionally, snails seemed to be extremely active during rainy weather that followed several days of dry weather (personal observation).

Prolonged periods of dry weather may be stressful for snails and precipitation following such conditions may stimulate a high proportion of the snail population to be active on the litter surface. This behaviour, coupled with the tendency for snails to be in the upper 5cm of the litter (Locasciulli and Boag, 1987), suggests that late summer and early autumn are likely favourable times for transmission.

Monthly size class distributions of E. fulvus indicated that juvenile recruitment was not accompanied by a noticeable die-off of large, older snails. The prevalence of infection in E. fulvus snails increased with increasing shell size, juvenile snails having the lowest prevalence of infection. There was no correlation between shell size and intensity of infection for E. fulvus snails. Possibly these snails lose larvae over time or the more heavily infected snails die. Snails were often infected concurrently with second- and third-stage larvae suggesting that reinfection can occur when conditions are favourable for snail activity and larval activity.

Pupillid species demonstrated a narrow range of shell width measurements making it difficult to examine prevalence of infection by size class. Although juvenile pupillids were collected in all months examined, they were few in number. Such a relatively low prevalence of juvenile pupillids may be explained by several possible factors; 1) habitat segregation between juvenile and adult stages; 2) a

rapid maturation rate of juvenile snails; and 3) long life and low juvenile recruitment of pupillids. Kralka (1984a) studied V. gouldi in the boreal forest in Alberta and concluded that they likely had a stable population, juvenile recruitment occurred during most of the summer and was not associated with a die-off of older snails.

Monthly size class distributions of both E. fulvus and pupillid snails indicated overwinter survival of all size classes. Overwinter survival of the intermediate host snail species at Sheep River, and the continued presence of juvenile stages are characteristics that have been suggested to represent stable gastropod populations in temperate regions (Mason, 1970).

Samuel et al. (1985) determined that an autumn transmission period occurred in the life cycle of Parelaphostrongylus odocoilei, a protostrongylid nematode of northern populations of mule deer. However, the main intermediate host for P. odocoilei is a slug, Deroceras laeve, an annual species (Platt, 1980). A relatively long-lived intermediate host might result in a less clearly defined period of parasite transmission. Little is known about longevity of snail host species at Sheep River, but over-winter survival of all size classes of the E. fulvus and pupillid snails indicates these species live at least one year and probably longer, suggesting that transmission of bighorn sheep lungworm is not concentrated in a short

'window' of exposure. As well, the assumed ability of P. stilesi/rushi to use several snail species as intermediate hosts, and the possibility that rate of larval development differs between snail species (as has been suggested by Halvorsen and Skorping (1982) for the life cycle of E. rangiferi), suggests that P. stilesi/rushi may use several transmission strategies.

Samson and Holmes (1985) found that P. stilesi/rushi larvae infecting the laboratory host Vallonia pulchella, did not develop at temperatures below 8°C. They concluded that development of protostrongylid larvae infecting 'field' intermediate host snails was unlikely during winter months. Instead, development would occur primarily during the spring and summer. Samson (1984) also found that larvae in snails that were kept at a cool temperature, then moved to a warm temperature, developed faster than expected. What causes this elevated rate of larval development is unknown. However, this finding suggests that second-stage larvae infecting snails entering hibernation in autumn, may experience rapid development when the snails emerge in spring.

Second and third-stage larvae were not found in pupillid snails that were experimentally exposed to P. stilesi/rushi during September 1984, then released in an aspen copse at Sheep River until approximately 28 May, and late August, 1985, respectively (see Appendix II). Thi

rate of larval development is considerably slower than what has been predicted by Samson and Holmes (1985). Confinement of the pupillid snails to enclosures during unfavourable weather conditions in summer may have increased the duration and frequency of inactivity and/or estivation, which could in turn have prolonged larval development. Also, the rate of larval development in pupillids may be longer than what has been noted for the vallonid snail V. pulchella. Rate of development of protostrongylid larvae differs in different species of intermediate hosts (Lankester and Anderson, 1968; Urban, 1980).

Unlike the development of larvae in the pupillids, which was slow, development of protostrongylid larvae in Vitrina alaskana was rapid, as revealed by the two snails infected with third-stage protostrongylid larvae in September, 1985. Members of the family Vitrinidae are believed to have an annual life cycle (Uminski and Focht, 1979). This is supported by Boag and Wishart (1982), who suggested that Vitrina alaskana at Sheep River may overwinter at the egg stage. During the present study no juveniles were collected until late June. Rate of larval development in V. alaskana may have been influenced by the lack of noticeable 'estivation' behaviour observed for this species. Regardless of the environmental conditions, V. alaskana snails could be collected from permanent plots. During periods when the major intermediate host species were

scarce, V. alaskana snails were active.

Snail density in the litter increased with increased precipitation. Likewise, a trend existed between the weekly number of major intermediate host snails/permanent plot and precipitation suggesting that precipitation is an important environmental factor influencing snail activity. The role of precipitation in influencing snail activity is supported by Boag (1985) who found humidity to be the most important overall condition affecting the activity of snails housed in terraria.

The high frequency of infected snails and low abundance of intermediate host species during autumn suggests the possibility of a behavioural difference between infected and uninfected snails. The large adult snails that make up the majority of infected snails in autumn possibly remain active in the surface litter longer than uninfected snails. Whether or not this could be attributed to snail infection or snail age is unknown, but snails infected with P. stilesi/rushi are more active than uninfected snails (Samson, 1984). The relatively high frequency of infection noted in April 1985 and the lower prevalence in May 1985 may result from infected snails emerging from hibernation before uninfected snails.

Observations of sheep in the aspen-grass sites during autumn indicated that they commonly ate the vegetative heads of the grasses, not the stems, and/or browsed on the leaves

of small aspen trees growing in the aspen-edge areas. Only where the grass was kept mowed (the Ranger Station lawn), were sheep observed to crop the vegetation close to the ground. During spring, new growth of the grasses is at the plant base. Sheep tend to feed on new vegetative growth during spring, bringing them in close contact with leaf litter, and possibly the infective snails active at this time. Litter samples collected in early March 1984 contained active snails. As the leaf litter was still partially frozen, snail activity prior to collection was unlikely. This suggests that snails do hibernate in leaf litter, and these snails would be available to bighorn sheep in the spring.

The timing of bighorn sheep return to the winter range in autumn is more variable than when they leave in spring. The Sheep River herd generally returned to their winter range in October, but for the last 5 years, they have been returning as early as mid-August (Festa-Bianchet, 1986). Spring departure from the winter range has remained predictable (13 May - 19 May), reflecting ewe migration to the lambing grounds.

Sheep returning to the winter-range in late September or early October likely have a lower potential exposure to infective snails due to probable snow cover and cold temperatures, factors that minimize snail availability and activity (Boag and Wishart, 1982). In very early September

1985, snails were collected from permanent plots, but after the first snow storm (6 Sept.) no snails were recovered even though the snow had melted and the ground was moist.

Sheep returning to the winter range earlier than usual should have increased exposure to lungworm infection. Festa-Bianchet (1987) found a relationship between early (= before 15 Sept.) return to the winter range and increased larval output during 1982 and 1983, but not during 1984. Sheep returning to the winter range late in the autumn (= after 15 Sept) should have reduced exposure to lungworm infection. Festa-Bianchet (1987) studied 13 ewes that returned to the winter range early one year and late another year and found that ewes returning late experienced a greater reduction in transformed LPG than those returning early. As intensity of larval output in individual sheep is probably influenced by several factors, such as the immune response and condition of a sheep (Festa-Bianchet, 1987), significant differences between larval output of early returning sheep and late returning sheep remains unclear.

Samson et al. (1987, in press) found that 21 of 44 lambs from Ram Mountain, Alberta, demonstrated probable transplacental infection, suggesting that this mode of transmission is common. Spraker and Hibler (1982) proposed that lungworm infection is an important mortality factor when lambs are transplacentally infected. Although Festa-Bianchet (1987) found ewes with high larval output had less

viable lambs, fetuses from high larval output ewes at Sheep River demonstrated low levels of transplacental infection (1 - 4 third-stage larvae) (Festa-Bianchet and Samson, 1984). Festa-Bianchet (1987) concluded that body condition of the ewe and stress and/or malnutrition of the lamb are important factors affecting lamb mortality, the role of transplacental infection affecting lamb mortality at Sheep River being unclear.

Lungworm availability values calculated for spring, summer, and autumn 1984, indicated that autumn and spring are important times for lungworm transmission to bighorn sheep. The prevalence of infective snails and intensity of infection was highest during autumn. However, snail density during autumn 1984 was relatively low; possibly snails had begun to hibernate. Although the prevalence of infective snails and intensity of infection was low during spring, snail density was high, probably reflecting snails emerging from hibernation.

Both autumn and early spring are favourable for the transmission of lungworm to bighorn sheep: infective snails are active, and sheep are present and concentrated on the winter range. It is difficult to define clearly which in either season is the major transmission period. The apparent stability of the intermediate host populations, and their frequency of infection, suggests that the transmission of lungworm to bighorn sheep may not be dependent on the

population dynamics of the intermediate host species. Instead, the feeding behaviour of the sheep and environmental conditions enhancing snail activity are more likely to play a major role.

Location of transmission

The relative frequency of infective snails was highest in the aspen-center and aspen-edge habitat types during summer 1984, autumn 1984, and spring 1985 for the permanent plot data. Habitat distribution of infected snails was similar to that of uninfected snails; snails were most abundant in the aspen-center and aspen-edge areas. When seasonal data were combined, the prevalence of infected snails was high in the grass-center habitat, suggesting a possible difference in the habitat distribution of infected and uninfected snails. However, grass-center areas had low snail density and snails collected in this habitat were generally large F. fulvus, probably better able to move the long distances than small snails.

A significantly higher proportion of snails were collected from the grass-edge areas than the other habitat types during May, 1984. Weather data at this time indicated that snails were found in these areas after 9 days of continuous rainfall, which probably encouraged snail

activity. Because conditions were favourable in the grass-edge and center habitats, snails may have been able to migrate to these areas without encountering unfavourable conditions.

Observations of bighorn sheep behaviour on the winter range during autumn, indicated that sheep were frequently present in aspen-edge and center areas. During the observation period there were several days of heavy rainfall; e.g., a total of 93 mm precipitation was recorded on September 12, 1985. Scans of sheep were difficult during such weather as they seemed to 'disappear' from the range. Glimpses of sheep indicated that some of the herd often took shelter in aspen copses, which seems an ideal time for lungworm transmission to occur. Unfortunately, observations of sheep use of the habitat types were not obtained for spring. However, observations by Festa-Bianchet (1982) indicated that sheep continue to use aspen copses in spring. Bighorn sheep use aspen copses during autumn and spring, overlapping the habitats where infected snails were available. Although aspen-edge and grass-edge habitats had high index values during autumn it is not clear if an autumn transmission period is more important than spring.

The effect of moisture on Protostrongylus stilesi/rushi development in the laboratory host Vallonia pulchella

Samson and Holmes (1985) determined that P. stilesi/rushi larvae development was temperature dependent. When infected Vallonia pulchella were maintained at 30°C they found that third-stage larval development occurred 14 days post-exposure, identical to results of the present study for snails in the wet regime. How behaviour of the snail hosts influences the rate of lungworm development and, thus, transmission, is unknown. Differing rates of larval development between the moisture regimes might have been influenced by the feeding behaviours of the experimental snails; wet regime snails were active and fed throughout the experiment (determined by presence of material in the gut tract and observations of faecal material), while dry regime snails were inactive and did not feed. The affect of starvation of snails on the development rate of Elaphostrongylus rangiferi larvae (Skorping, 1984) lends support to the supposition that differing rates of development observed between the moisture regimes were affected by the nutritional status of the experimental snails. Development of larvae in naturally infected snails may be affected by this and other factors.

Possible transmission patterns

When on the winter range at Sheep River, bighorn sheep produce high levels of first-stage P. stilesi/rushi lungworm larvae (Uhazy et al., 1973). Feeding behaviour of bighorn sheep brings them in contact with aspen copses (Festa-Bianchet, 1982) that they 'seed' with first-stage lungworm larvae (Boag and Wishart, 1982). Snail species that are lungworm intermediate hosts are most numerous in aspen-copse habitats on the winter range (Boag and Wishart, 1982; Locasciulli and Boag, 1987; this study). Snail infection probably occurs when environmental conditions favour snail activity, suggested by the presence of second-stage larvae in infected snails throughout the year. Longevity of the snail hosts, overwinter survival of infected snails, and the high proportion of infected snails that are adults, suggests that the prevalence of infected snails in the snail population is relatively stable throughout the year.

Bighorn sheep migrate to the summer range in mid-May and return to the winter range in mid-August. Although the date of migration to the summer range is relatively consistent, the date of return to the winter range is variable. Lungworm availability values were highest in aspen-center and aspen-edge habitats during spring and aspen-edge and grass-edge habitats during autumn. Sheep feeding in these habitats become infected when they

accidentally ingest active infective snails, and/or infective snails still hibernating in the litter. If sheep are in poor body condition in the spring, success of lungworm establishment may be enhanced.

Stability of the snail intermediate host population, and frequency of infection, and the use of aspen-copses by bighorn sheep, suggests that accidental ingestion of snails by bighorn sheep is affected by environmental conditions that increase snail activity. Snail activity, the amount of time sheep are present on the winter range, and the feeding behaviour of bighorn sheep are likely the most important factors for lungworm transmission during autumn and spring.

Two modes of transmission have been proposed for the bighorn sheep-lungworm life cycle, 1) accidental ingestion of infected snails by bighorn sheep, and 2) transplacental transmission to a fetus when a pregnant ewe accidentally ingests an infected snail (Hibler et al., 1982).

Accidental ingestion of infected snails can occur during autumn and spring. Although larval 'storage' by the ewe, until such time that the larvae are transplacentally transmitted to the fetus, has been proposed by Hibler et al. (1982), this strategy does not seem necessary given the availability of infective snails during spring.

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APPENDICES

Appendix I

Exposure of mule deer fawns to protostrongylid-infected snails from Sheep River

Introduction

In an attempt to determine the identity of protostrongylid-type larvae in snails from Sheep River, four mule deer fawns were fed naturally infected snails collected from Sheep River. This appendix summarizes results.

Methods

Fawns, approximately 3 weeks old, were housed at the University of Alberta Ellerslie Research Station. They were maintained following procedures of Pybus 1983 (Parelaphostrongylus andersoni Prestwood 1972 and P. odocoilei (Hobmaier and Hobmaier, 1934) (Nematoda: Metastrongyloidea) in two cervid definitive hosts. Ph.D. Thesis, University of Alberta, Edmonton. 185pp.). Infected intermediate host snails collected from Sheep River in April-June in 1985 were fed to mule deer fawns per os. The snail species Euconulus fulvus (n L3 = 48), Vertigo gouldi (n L3 = 48), Vertigo modesta (n L3 = 27), and a member of the family Succineidae (n L3 = 14) were used in the experimental infections. Each of the four experimental fawns were fed infective snails of only one of the species. Additionally, a control fawn was exposed to laboratory-

infected Vallonia pulchella containing 50 P. stilesi/rushi L3 larvae. A second control fawn received laboratory-infected V. pulchella containing 35 O. macrotis L3 larvae.

Fawns were terminated 32 to 42 days post exposure. The lungs were examined for nematode infection in two ways: first by flushing with saline solution, screening the saline flushed from the lungs, and examining the screenings, and second by cutting open the bronchioles and examining the exposed surfaces.

Results

Nematodes were recovered from two fawns, one a control and one experimental. Two worms, Orthostrongylus macrotis, were recovered from the control fawn infected with Orthostrongylus macrotis. One worm, Orthostrongylus macrotis, was recovered from the experimental fawn exposed to infective Vertigo modesta. In both of the infected fawns the lungs appeared healthy and did not demonstrate noticeable pathology.

Appendix II

Protostrongylus stilesi/rushi development in laboratory infected *Vertigo* spp. snails housed under natural conditions

Introduction

The rate of protostrongylid larval development in snail intermediate hosts, housed under natural conditions, was examined to help determine the timing of lungworm transmission to bighorn sheep.

Methods

A total of three hundred uninfected adult stage *Vertigo* spp. snails was collected from aspen-copses at Sheep River during 13 September, 1984. All snails were marked with model paint for future identification. *Vertigo* spp. snails were exposed to 16 000 first-stage *Protostrongylus stilesi/rushi* larvae for 2 1/2 hours, following the procedure for snail exposure outlined in the methods section.

Six metal cylinders 24cm x 20cm were sunk into the ground in the center of an aspen copse, a 4cm rim was left above ground. Thirty marked *Vertigo* spp. snails were released in each cylinder enclosure on 14 September, 1984. Commencing 28 May, 1985, snails were periodically removed from the enclosures and examined for presence and developmental stages of protostrongylid larvae.

A second group of 120 Vertigo spp. snails was collected and released on 3 June 1985, these snails were exposed to P. stilesi/rushi and released in the aspen copse enclosures as before. Commencing 22 June these snails were periodically collected from enclosures and examined for protostrongylid infection.

Results

Vertigo spp. snails exposed to Protostrongylus stilesi/rushi larvae in September 1984 did not demonstrate third-stage larvae until the end of August 1985 (Table I), much longer than previously predicted by Samson and Holmes (1985. Can. J. Zool. 63:1445-1448.). A relatively slow rate of larval development was similarly observed for snails exposed in June 1985 (Table II).

Table 1. Development of P. stilesi/rushi larvae in Vertigo spp. snails exposed to P. stilesi/rushi larvae on September 14, 1984.

Date examined	n snails examined	n infected with L2	n infected with L3
May 28, 1985	14	10	0
June 5	3	3	0
June 13	6	6	0
July 15	3	3	0
August 30	4	0	4

Table II.[1] Development of *P. stilesi/rushi* larvae in *Vertigo* spp. snails exposed on 3 June, 1985.

Date examined	*n* snails examined	*n* infected with l2	*n* infected with l3
June 22	4	0	0
August 30	1	1	0

Appendix III. Weekly precipitation, temperature, #snails/permanent plot, and #snails/m^2 values from Sheep River in 1984.

Date	ppt (mm)	$\bar{x}$ °C	# snails per plot	# of plots	# snails per m^2	# of samples
16/5/84-22/5/84	2.0	17.0	0.07	480	21.66	24
23/5/84-29/5/84	37.5	19.7	0.25	480	10.82	24
30/5/84-5/6/84	28.0	15.6	0.07	480	14.16	24
6/6/84-12/6/84	76.0	14.6	1.86	422	89.16	24
13/6/84-19/6/84	26.0	19.7	0.42	480	5.83	36
20/6/84-26/6/84	46.0	18.1	0.65	480	44.16	24
27/6/84-3/7/84	0.0	21.5	0.17	480	16.66	24
4/7/84-10/7/84	0.0	18.6	0.04	366	8.33	24
11/7/84-17/7/84	0.0	24.7	0.04	648	24.16	24
18/7/84-24/7/84	11.0	23.8	0.26	480	0.00	24
25/7/84-31/7/84	17.0	25.1	1.86	592	15.82	24
1/8/84-7/8/84	14.0	24.5	2.10	366	0.00	24
8/8/84-14/8/84	0.0	24.3	0.00	480	0.00	24

Appendix IV. Monthly number of snails collected; prevalence of infection, and mean intensity of infection values for the snail species Euconulus fulvus (E.f.), Vertigo gouldi (V.g.), Vertigo modesta (V.m.), Columella spp. (Col.), Immature pupillid (I.P.), Vertigo spp. (V.spp.), and Cationella sp. (Cat.) in the habitats aspen-center (AC), aspen-edge (AE), grass-edge (GE), and grass-center (GC) from litter sample data collected at Sheep River in 1984.

Month/Habitat	Snail Species						
	E.f.	V.g.	V.m.	Col.	I.P.	V.spp.	Cat.
APRIL/AC							
#coll.	10	29	6	1	4	8	0
prevalence	0	0	0	0	0	0	0
$\bar{x}$ intensity	0	0	0	0	0	0	0
/AE							
#coll.	2	14	4	1	2	0	0
prevalence	0	.07	.25	0	0	0	0
$\bar{x}$ intensity	0	1.0	2.0	0	0	0	0
/GE							
#coll.	0	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
$\bar{x}$ intensity	0	0	0	0	0	0	0
/GC							
#coll.	0	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
$\bar{x}$ intensity	0	0	0	0	0	0	0
MAY/AC							
#coll.	26	50	2	1	16	9	0
prevalence	.04	.04	0	0	0	.11	0
$\bar{x}$ intensity	2.0	3.0	0	0	0	1.0	0
/AE							
#coll.	32	40	1	1	11	6	0
prevalence	0	.02	0	0	0	0	0
$\bar{x}$ intensity	0	1.0	0	0	0	0	0
/GE							
#coll.	0	4	0	0	1	0	0
prevalence	0	0	0	0	0	0	0
$\bar{x}$ intensity	0	0	0	0	0	0	0
/GC							
#coll.	2	1	0	0	0	0	0
prevalence	0	0	0	0	0	0	0

Month/Habitat	Snail Species						
	E.f.	V.g.	V.m.	Col.	I.P.	V.spp.	Cat.
x̄ intensity	0	0	0	0	0	0	0
/AC							
#coll.	13	28	10	1	2	0	0
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0
/AE							
#coll.	39	41	21	9	39	2	0
prevalence	.02	.02	.05	0	.02	0	0
x̄ intensity	2.0	1.0	1.0	0	1.0	0	0
/GE							
#coll.	1	7	2	0	0	1	0
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0
/GC							
#coll.	0	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0
JULY/AC							
#coll.	4	4	0	0	1	3	3
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0
/AE							
#coll.	9	3	1	0	0	2	0
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0
/GE							
#coll.	1	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0
/GC							
#coll.	0	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0
SEPT.& OCT. /AC							
#coll.	1	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0

Month/Habitat	Snail Species						
	E.f.	*V.g.*	*V.m.*	*Col.*	I.P.	*V.spp.*	*Cat.*
/AE							
#coll.	2	5	0	0	0	0	0
prevalence	.50	.60	0	0	0	0	0
$\bar{x}$ intensity	1.0	7.6	0	0	0	0	0

Appendix V. Monthly number of snails collected, prevalence of infection, and mean intensity of infection values for the snail species Euconulus fulvus (E.f.), Vertigo gouldi (V.g.), Vertigo modesta (V.m.), Columella spp. (Col.), Immature pupillid (I.P.), Vertigo spp. (V.spp.), and Cationella sp. (Cat.) in the habitats aspen-center (AC), aspen-edge (AE), grass-edge (GE), and grass-center (GC) from permanent plot data collected at Sheep River in 1984.

Month/Habitat	Snail Species						
	E.f.	V.g.	V.m.	Col.	I.P.	V.spp.	Cat.
MAY/AC							
#coll.	26	15	12	3	3	2	0
prevalence	.07	0	.16	0	0	0	0
x̄ intensity	8.0	0	1.5	0	0	0	0
/AE							
#coll.	9	23	27	7	5	1	1
prevalence	.22	0	.04	0	0	1.0	0
x̄ intensity	4.5	0	1.0	0	0	6.0	0
/GE							
#coll.	4	1	0	1	0	0	0
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0
/GC							
#coll.	0	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
x̄ intensity	0	0	0	0	0	0	0
JUNE/AC							
#coll.	117	161	162	13	46	14	0
prevalence	.05	.05	.04	.07	.04	.14	0
x̄ intensity	2.5	4.0	1.7	3.0	2.0	5.5	0
/AE							
#coll.	125	119	134	3	28	15	2
prevalence	.04	.02	.03	0	0	0	.50
x̄ intensity	1.8	2.3	2.2	0	0	0	1.0
/GE							
#coll.	25	15	7	0	1	2	0
prevalence	.08	.13	0	0	1.0	0	0
x̄ intensity	2.0	1.0	0	0	1.0	0	0
/GC							
#coll.	27	0	0	0	0	0	3
prevalence	.11	0	0	0	0	0	.33

Month/Habitat	Snail Species						
	E.f.	V.g.	V.m.	Col.	I.P.	V.spp.	Cat.
$\bar{x}$ intensity	7.0	0	0	0	0	0	4.0
/AC							
#coll.	67	159	174	17	18	12	0
prevalence	.04	.06	.03	0	.05	.08	0
$\bar{x}$ intensity	2.3	3.1	1.2	0	1.0	16.0	0
/AE							
#coll.	57	109	208	15	26	17	1
prevalence	.03	.05	.03	0	.04	.12	1.0
$\bar{x}$ intensity	1.5	2.2	1.2	0	1.0	6.0	8.0
/GE							
#coll.	7	11	11	0	0	0	0
prevalence	0	.09	.09	0	0	0	0
$\bar{x}$ intensity	0	1.0	1.0	0	0	0	0
/GC							
#coll.	3	0	1	0	0	0	0
prevalence	.33	0	1.0	0	0	0	0
$\bar{x}$ intensity	1.0	0	5.0	0	0	0	0
AUGUST/AC							
#coll.	25	73	137	5	0	11	0
prevalence	.20	.01	.01	0	0	0	0
$\bar{x}$ intensity	1.6	1.0	1.0	0	0	0	0
/AE							
#coll.	25	90	192	5	9	11	0
prevalence	.08	.05	.01	.20	0	0	0
$\bar{x}$ intensity	2.5	3.0	2.3	1.0	0	0	0
/GE							
#coll.	1	6	1	0	0	1	0
prevalence	0	0	0	0	0	0	0
$\bar{x}$ intensity	0	0	0	0	0	0	0
/GC							
#coll.	4	0	0	0	0	0	0
prevalence	.25	0	0	0	0	0	0
$\bar{x}$ intensity	3.0	0	0	0	0	0	0
SEPTEMBER/AC							
#coll.	26	52	26	6	11	2	0
prevalence	.07	.06	.07	0	.09	1.0	0
$\bar{x}$ intensity	9.0	2.0	1.5	0	4.0	1.5	0

Month/Habitat	Snail Species						
	E.f.	*V.g.*	*V.m.*	*Col.*	I.P.	*V.*spp.	*Cat.*
/AE							
#coll.	43	25	28	4	2	0	0
prevalence	.05	.16	0	0	.50	0	0
$\bar{x}$ intensity	2.0	1.5	0	0	1.0	0	0
/GE							
#coll.	3	10	1	0	1	0	0
prevalence	0	.10	0	0	0	0	0
$\bar{x}$ intensity	0	1.0	0	0	0	0	0
/GC							
#coll.	2	0	2	0	0	0	1
prevalence	.50	0	.50	0	0	0	1.0
$\bar{x}$ intensity	4.0	0	4.0	0	0	0	1.0
OCTOBER/AC							
#coll.	8	1	0	0	0	0	0
prevalence	.50	0	0	0	0	0	0
$\bar{x}$ intensity	8.5	0	0	0	0	0	0
/AE							
#coll.	1	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
$\bar{x}$ intensity	0	0	0	0	0	0	0
/GE							
#coll.	0	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
$\bar{x}$ intensity	0	0	0	0	0	0	0
/GC							
#coll.	0	0	0	0	0	0	1
prevalence	0	0	0	0	0	0	0
$\bar{x}$ intensity	0	0	0	0	0	0	0

Appendix VI. Monthly number of snails collected, prevalence of infection, and mean intensity of infection values for the snail species Euconulus fulvus (E.f.), Vertigo gouldi (V.g.), Vertigo modesta (V.m.), Columella (Col.), Immature pupillid (I.P.), Vertigo spp. (V.spp.), and Cationella sp. (Cat.) in the habitats aspen-center (AC), aspen-edge (AE), grass-edge (GE), and grass-center (GC) from permanent plot data collected at Sheep River in 1985.

Month/Habitat	Snail Species						
	E.f.	V.g.	V.m.	Col.	I.P.	V.spp.	Cat.
APRIL/AC							
#coll.	16	43	14	0	2	4	0
prevalence	.12	.05	.07	0	0	0	0
$\bar{x}$ intensity	1.5	1.0	1.0	0	0	0	0
/AE							
#coll.	16	19	5	0	3	3	0
prevalence	.12	.16	0	0	0	0	0
$\bar{x}$ intensity	4.5	3.0	0	0	0	0	0
/GE							
#coll.	6	2	2	0	0	1	0
prevalence	.16	.50	0	0	0	0	0
$\bar{x}$ intensity	4.0	2.0	0	0	0	0	0
/GC							
#coll.	0	0	0	0	0	0	0
prevalence	0	0	0	0	0	0	0
$\bar{x}$ intensity	0	0	0	0	0	0	0
MAY/AC							
#coll.	87	173	192	4	18	12	0
prevalence	.05	.05	.02	0	0	0	0
$\bar{x}$ intensity	1.0	1.8	4.3	0	0	0	0
/AE							
#coll.	134	181	239	1	16	14	0
prevalence	.04	.08	.03	0	0	0	0
$\bar{x}$ intensity	1.2	2.3	1.8	0	0	0	0
/GE							
#coll.	22	26	4	0	0	0	1
prevalence	.09	.07	0	0	0	0	0
$\bar{x}$ intensity	2.6	2.5	0	0	0	0	0
/GC							
#coll.	4	0	1	0	0	0	5
prevalence	.25	0	0	0	0	0	.20

Month/Habitat	Snail Species						
	E.f.	V.g.	V.m.	Col.	I.P.	V.spp.	Cat.
$\bar{x}$ intensity	1.0	0	0	0	0	0	17.0
JUNE/AC							
#coll.	81	56	100	2	9	13	0
prevalence	.10	.05	.01	0	0	0	0
$\bar{x}$ intensity	3.1	1.3	2.0	0	0	0	0
/AE							
#coll.	87	65	130	4	12	0	0
prevalence	.07	.06	.02	0	0	0	0
$\bar{x}$ intensity	1.3	3.8	1.3	0	0	0	0
/GE							
#coll.	18	5	1	0	0	0	1
prevalence	.05	.20	0	0	0	0	1.0
$\bar{x}$ intensity	4.0	1.0	0	0	0	0	4.0
/GC							
#coll.	7	0	0	0	0	0	0
prevalence	.14	0	0	0	0	0	0
$\bar{x}$ intensity	1.0	0	0	0	0	0	0

Appendix VII. Total lengths of third-stage protostrongylid larvae from infected snails collected at Sheep River in 1984.

Snail Species	Habitat	Snail Size(mm)	L3 Total Length (μm)
E. fulvus	AC	3.3	420
E. fulvus	AC	2.3	600
E. fulvus	AC	2.4	550, 576, 578, 530, 546
E. fulvus	AC	2.6	474, 486, 462
E. fulvus	AC	3.0	508, 534, 516, 548, 554, 534, 494, 508, 460, 486, 510
E. fulvus	AC	2.8	486, 504, 554 448, 510
E. fulvus	AC	2.6	470
E. fulvus	AE	2.7	558, 392
E. fulvus	AE	2.9	500
E. fulvus	AE	1.7	510, 530
E. fulvus	AE	2.9	542
E. fulvus	AE	1.9	560
E. fulvus	GE	2.6	468, 574
E. fulvus	GE	2.1	410, 520
E. fulvus	GC	3.1	554
E. fulvus	GC	2.6	520, 518, 566, 592
V. gouldi	AC	1.8	510, 548
V. gouldi	AC	1.9	536
V. gouldi	AC	1.8	554, 520, 592, 518
V. gouldi	AC	1.9	546, 556, 520
V. gouldi	AC	1.8	556
V. gouldi	AE	2.1	610, 570
V. gouldi	AE	2.0	530
V. gouldi	AE	1.8	578
V. gouldi	AE	1.7	586
V. gouldi	AE	1.8	352
V. gouldi	AE	1.8	540
V. gouldi	AE	1.9	370
V. gouldi	AE	2.0	442
V. gouldi	AE	2.0	544, 538, 464, 556
V. gouldi	AE	1.9	542
V. gouldi	AE	1.8	476
V. gouldi	GE	1.9	500
V. gouldi	GE	1.7	560
V. gouldi	GE	1.9	592
V. gouldi	GE	1.9	468, 530

Snail Species	Habitat	Snail Size(mm)	L3 Total Length (μm)
V. modesta	AC	2.1	604
V. modesta	AC	2.2	540
V. modesta	AC	2.0	588, 540
V. modesta	AC	2.1	502
V. modesta	AC	1.8	547
V. modesta	AE	2.0	514
V. modesta	AE	1.9	475
V. modesta	AE	2.1	522
V. modesta	AE	2.1	550, 512, 540
V. modesta	AE	2.0	596
V. modesta	AE	1.9	450, 441
V. modesta	AE	2.2	606
V. modesta	GE	1.9	520
V. modesta	GE	2.1	706, 540, 664, 580
V. modesta	GC	1.7	520
V. modesta	GC	2.1	536
Imm. Pupillid	AC	1.6	469
Imm. Pupillid	AC	1.3	570
Imm. Pupillid	AC	1.6	606
Imm. Pupillid	AC	1.2	452
Imm. Pupillid	AE	1.2	470
Vertigo spp.	AC	1.9	516
Vertigo spp.	AC	1.6	564
Vertigo spp.	AE	1.8	386
Vertigo spp.	AE	1.8	474, 514, 528
Catinella sp.	GC	5.1	540, 524
Columella spp.	AE	2.0	552
D. cronkhitei	AC	3.3	461
D. cronkhitei	GE	4.4	550