UNIVERSITY OF ALBERTA

Meningeal worm, Parelaphostrongylus *tenuis* (Nematoda), in Manitoba, Saskatchewan and North Dakota: distribution and ecological correlates.

BY

SHAWN M. WASEL ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

DEPARTMENT OF ZOOLOGY

Edmonton, Alberta
Fall 1995

ISBN 0-612-06554-5

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: SHAWN M. WASEL

TITLE OF THESIS: MENINGEAL WORM, *PARELAPHOSTRONGYLUS TENUIS* (NEMATODA), IN MANITOBA, SASKATCHEWAN AND NORTH DAKOTA: DISTRIBUTION AND ECOLOGICAL CORRELATES

DEGREE: MASTER OF SCIENCE

YEAR THIS DEGREE GRANTED: Fall 1995

316A Willow Drive
Sunset Beach, Alberta
T9S 1R6

DATE: MAY 26, 1995

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled MENINGEAL WORM, *PARELAPHOSTRONGYLUS TENUIS* (NEMATODA), IN MANITOBA, SASKATCHEWAN AND NORTH DAKOTA: DISTRIBUTION AND ECOLOGICAL CORRELATES submitted by SHAWN M. WASEL in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

W. M. Samuel (Supervisor)

M. Belosevic

R.J. Hudson

Date: MAY 26, 1995

Abstract

In an attempt to determine the northwestern distribution of meningeal worm (*Parelaphostrongylus tenuis*) in North America, 2186 white-tailed deer from Manitoba, Saskatchewan, and North Dakota were examined for presence of adult parasites. Prevalence was 18.6, < 1, and 8.4% in Manitoba, Saskatchewan, and North Dakota, respectively. Relationships of sex and age of deer with prevalence and intensity of infection were examined. Prevalence was not significantly different between sexes and increased with age of deer. Intensity of infection did not differ significantly between sex or age of deer. Associations of presence and prevalence of *P. tenuis* with precipitation, temperature, presence of suitable intermediate hosts, white-tailed deer density and forested land were explored using linear and logistic regression analysis. Presence of *P. tenuis* was positively correlated with precipitation during frost-free periods and deer density. There was a negative correlation between presence of *P. tenuis* and winter temperature. Gastropod intermediate hosts were most abundant and well distributed in regions of the study area with the highest reported prevalence. Landscapes with less than 75% and greater than 50% forest cover were most likely to have *P. tenuis* infected deer. Summer precipitation, fall precipitation, winter temperature, spring temperature and percent forested land, using stepwise multiple logistic regression analysis, provided the highest explanatory power for predicting the presence of *P. tenuis* ($r^2 = 0.56$). A positive correlation between prevalence of the parasite and fall and winter precipitation was found in North Dakota only. Annual changes in climate were not significantly associated with annual changes in prevalence. The westernmost limit of *P. tenuis* is likely restricted by low rainfall, low white-tailed deer density and limited abundance and distribution of terrestrial gastropods. The influence of temperature on distribution remains unclear, however, threshold temperatures (both low and high) for transmission are likely. In conjunction with other ecological variables, I propose that higher temperatures associated with the grassland biome limits distribution of the parasite by restricting distribution of the intermediate host; cooler temperatures associated with the northern boreal mixedwood forest limits distribution of *P. tenuis* by retarding gastropod activity and development of *P. tenuis* larvae within the gastropod host. Management implications with respect to accidental introduction and natural spread of *P. tenuis* are discussed.

Acknowledgments

Thanks are extended to the many hunters, meat cutting shops, hunting clubs and personnel of Manitoba, Saskatchewan and North Dakota game management agencies. The list of individuals that contributed to this project is lengthy and at the risk of forgetting someone, I will not attempt to name them all. Individuals deserving special mention include Dr. Vince Crichton, Manitoba Department of Natural Resources, Wildlife Branch, who coordinated collection of deer heads in Manitoba and graciously provided his back yard in suburban Winnipeg as a repository for temporary storage of heads; Dr. Rex Sohn, Disease Research Supervisor, North Dakota Game and Fish Department, who helped coordinate collection efforts in North Dakota and ensured that clearance of customs with our unusual cargo went as smoothly as possible. Hugh Hunt, Saskatchewan Environment and Resource Management Department, coordinated collection efforts in Saskatchewan and helped with the onerous task of loading heads on a cold snowy February night. The immense task of coordinating the collection of over 2000 deer heads orchestrated by these individuals and departmental personnel was sincerely appreciated.

Chris Wilke and Dwight Welch provided much appreciated help in the often eventful, deep winter head collection runs that often coincided with a blizzard. Clarence Gerla, John Nishi, and Kelly Sturgess provided much help moving and storing deer heads. Alberta Fish and Wildlife Services, Forensic Laboratory personnel, Bob McClymont, and Bruce Treichel provided necropsy facilities and patiently accommodated many of the logistic problems associated with storage, necropsy and incineration of 2300 deer heads. Dr. Margo Pybus, Wildlife Disease Specialist, Alberta Fish and Wildlife Services, provided exceptional instruction, and shared skills used in effective search and recovery of *Parelaphostrongylus tenuis*.

The many hours in the necropsy room were much more enjoyable with the cheerful technical assistance of Laurie Hunt, Cathy McDougall, John Nishi, Kelly Sturgess and Chris Wilke. Dr. Al Shostak confirmed nematode identification and provided much appreciated assistance during data analysis and write-up. Sincere thanks are expressed to my supervisory committee, Drs. Mike Belosevic and Bob Hudson for their enthusiasm, encouragement and patience. A special thanks to Dr. Bill Samuel for teaching me about things you can't learn from any text book, his patience was thoroughly tested.

In-kind and monetary grants were provided by the Canadian Wildlife Federation, Alberta Fish and Wildlife Services, Saskatchewan Environment and Resource Management Department, North Dakota Game and Fish Department, Manitoba Wildlife Branch, and an NSERC operating grant to Dr. W.M. Samuel. Personal financial support was provided through a University of Alberta Teaching Assistantship, Research Assistantship, and an intersession bursary.

Lastly, I would like to thank my friends for their patience.

TABLE OF CONTENTS

List of Tables

Table **Page**

List of Figures

Figure **Page**

I) INTRODUCTION

In 1989, a 2-year study of meningeal worm (*Parelaphostrongylus tenuis*) was initiated in an attempt to provide additional information for game managers on distribution and ecology of this parasite. A specific goal was to assess the potential for natural range expansion of this pathogenic nematode into western North America. The three objectives of the study were to: 1) define the current western-most distribution of *P. tenuis* in white-tailed deer (*Odocoileus virginianus*) in central North America (Saskatchewan (SK), Manitoba (MB) and North Dakota (ND)); 2) examine relationships of deer sex, age class, and density to prevalence and intensity of *P. tenuis* infections and; 3) determine if the presence of *P. tenuis* was correlated to any of the following five ecological factors: precipitation, temperature, presence of suitable intermediate hosts, white-tailed deer density, and forested land.

General Overview

Parelaphostrongylus tenuis is a parasitic nematode of its most common definitive host, the white-tailed deer (*Odocoileus virginianus*). In deer, adult worms are found primarily in the subdural space and cranial venous sinus (Anderson 1965). *Parelaphostrongylus tenuis* has a unique history in the literature because it has been well documented that no or little pathology is associated with infection in white-tailed deer (WTD), but such is not the case for other hosts (See bibliography of Samuel 1991). Thus, when ungulates such as moose (*Alces alces*), elk (*Cervus elaphus*), caribou (*Rangifer tarandus*), llamas (*Llama glama*), and fallow deer (*Dama dama*) become infected, severe neurologic disease and death often result (Anderson 1965a, Carpenter et al. 1973, Baumgartner et al. 1985, Davidson et al. 1985, Bergerud and Mercer 1989) (Table 1). In these hosts, clinical signs of infection include: holding the head at an unusual angle, fearlessness, blindness, depression, circling and weakness in the hindquarters that may finally progress to paralysis and the inability to stand (Anderson and Prestwood 1981).

Parelaphostrongylus tenuis is found commonly in WTD throughout the deciduous mixed-wood forest of eastern North America. At present, it has been reported in the United States in: Alabama and Arkansas (Prestwood and Smith 1969), Connecticut (Nielson and Aftosmis 1964, only in sheep), Florida and Georgia (Prestwood and Smith 1969), Indiana (Platt 1989), Iowa (Jarvinen and Hedberg 1993), Kentucky (Davidson et al. 1985), Louisiana (Prestwood and Smith 1969), Maine (Behrend and Witter 1968, Gilbert 1973, Bogaczyk et al. 1993), Maryland (Prestwood and Smith 1969), Michigan (DeGiusti 1955 and 1963), Minnesota (Karns 1967), Mississippi (Prestwood and Smith 1969), New Hampshire (Thurston and Strout 1978), New Jersey (Pursglove 1977), New York (Behrend 1970, Garner and Porter 1991), North Carolina (Prestwood and Smith 1969), Oklahoma (Kocan et al. 1982), Pennsylvania (Beaudoin et al. 1970), South Carolina (Anderson and Prestwood 1981), Tennessee (Prestwood and Smith 1969), eastern Texas (domestic goats, see Guthery et al. 1979), Virginia (Dudak et al. 1965), West Virginia (Prestwood and Smith 1969), Wisconsin (Samuel and Trainer 1969); and from Canada in: Manitoba (Bindernagel and Anderson 1972), southern Ontario (Anderson 1963a), southern Quebec (Bindernagel and Anderson 1972), New Brunswick (Upshall et al. 1987), and Nova Scotia (Thomas and Dodds 1988).

Parelaphostrongylus tenuis has not been reported from, but is almost certainly present in Illinois, Delaware, Massachusetts, Ohio, Rhode Island, and Vermont, all states with many WTD and all surrounded by states with infected deer. It is rare or absent in the coastal plains of the southeastern U.S. where sandy soil and pine forests dominate (Comer et al. 1991), apparently absent from the interior great plains (Kocan et al. 1982) and prairie biome (Anderson 1972), areas with relatively high summer temperatures and low precipitation (Samuel and Holmes 1974), and absent from the boreal mixed-wood forest with its short growing season and relatively low densities of WTD.

With the recent advent of game ranching, and the associated translocation of ungulates throughout North America, the risk of accidental introduction of this pathogenic nematode to susceptible ungulate populations in the west, generated considerable controversy surrounding the game ranching industry (Samuel 1987, Samuel et al. 1992, Miller and Thorne 1993). In addition to relocation of ungulates associated with game ranching, state and provincial fish and wildlife agencies are frequently involved with removal and re-introduction of endemic ungulates into their former ranges. These re-introductions typically involve relocation of western-source moose, elk, and caribou into their former historic eastern ranges that are now inhabited by WTD known to be infected with *P. tenuis*. Prior to relocation of ungulates, game managers must carefully evaluate the following: presence of *P. tenuis*-infected WTD, susceptibility of ungulate species involved in the proposed introduction (*i.e.*, caribou), and any ecological overlap that may occur between infected WTD and the introduced ungulate spec[illegible] prior to the relocation. Introduction of a susceptible ungulate into *P. tenuis* range might result in the eventual failure of the introduction. *Parelaphostrongylus tenuis* has been implicated as a factor in the failure of a transplant of black-tailed deer (*Odocoileus hemionus columbianus*) from Oregon to Tennessee (Nettles et al. 1977) and of caribou reintroduction into Cape Breton National Park, Nova Scotia (Dauphine 1975). Bergerud and Mercer (1989) reviewed 33 introductions of caribou into eastern North America and concluded that caribou could not be successfully introduced into areas where WTD, with a high prevalence of *P. tenuis*, were present.

Knowledge of the distribution of *P. tenuis* is an important consideration even when proposing the relocation of clinically silent hosts such as WTD. Inadvertent relocation of *P. tenuis*, associated with the translocation of WTD, may facilitate the movement of *P. tenuis* across any natural ecological barrier that currently restricts this parasite to eastern North America. Once *P. tenuis* became established in local populations of WTD, it could have dire consequences for sympatric ungulate populations. Evidence substantiating the concern regarding *P. tenuis* "jumping" ecological barriers has been documented twice: 1) the single WTD infected with *P. tenuis*, reported from Collier County, Florida (Prestwood and Smith 1969), is now suspected to be the result of a translocation of Wisconsin-source, *P. tenuis*-infected, WTD introduced to the county in 1948 (Comer et al. 1991). This presumed accidental introduction of *P. tenuis* is based on distributionally disjunct, eastern-most report of *P. tenuis* associated with translocation of WTD; 2) the presence of *P. tenuis* on Wassaw Island (a national wildlife refuge), Georgia, is likely associated with the re-introduction of Pennsylvania-source, *P. tenuis* infected, WTD in 1905 - 1920. No WTD on nearby islands or the mainland are infected (W. R. Davidson pers. comm.).

In response to the threat of accidental introduction of *P. tenuis*, several western states and provinces prohibited the importation of non-endemic animals and/ or adopted tight controls to ensure that imported animals were free of the parasite (Kahn 1993, Miller and Thorne 1993). In addition to the obvious risk of translocating *P. tenuis* along with game ranched animals, some parasitologists (Bindernagel and Anderson 1972, Samuel and Holmes 1974, Shoesmith 1976) have expressed concern that *P. tenuis* may be expanding its range westward through the aspen parkland, eventually arriving in western North America where WTD occur sympatrically with susceptible, but uninfected, ungulate populations.

Study Area

This study encompassed the hypothesized northwestern range limit of *P. tenuis* in North America, which included the great plains, aspen parkland, deciduous and boreal mixed-wood forest regions of SK, MB and ND.

Topographic relief throughout the area is highly varied, ranging from the gentle rolling prairie of southern SK to the precipitous badlands along the little Missouri River in southwestern ND. Elevation ranges from 200m above sea level (ASL) along the Red River Valley in eastern ND and southeastern MB, to 800m ASL in the Turtle Mountains of ND and MB, Duck Mountains of MB, Missouri Plateau of southwestern ND and the Cypress Hills of southwestern SK.

The geophysical landscape of SK, MB and ND was influenced by three major geological events, the first of which occurred 100 million years before present (ybp), as thousands of meters of sediment were deposited when this region was covered by the Cretaceous Sea. The second geological event was the Rocky Mountain erogeny, which continued until 60-70 million ybp. This mountain building episode resulted in the erosion and scouring of sediments from the mountains and redeposition of these sediments onto the plains east of the front ranges of the Rocky Mountains. The third major geological event that had an important influence on the great plains boreal transition region was the continual advance and retreat of the glacial ice sheets during the Pleistocene (2 million ybp until 10 000 ybp). The scouring action of these moving ice sheets pulverized rock and deposited the rich fertile glacial sediments that are now found in southern SK and MB north of the 49th parallel, and in eastern ND south of the 49th parallel.

The climate of the region is described as interior continental climate. Annual precipitation and average annual temperature do not accurately represent the climate of this region. Of more importance is the frequency (how often does it rain or snow) and amplitude (how much does it rain or snow) of precipitation as well as year to year variation in average seasonal temperature. Long term dramatic annual fluctuations in precipitation (*i.e.*, drought) within the study area and frequent wildfires associated with these dry periods have been the major force that has influenced vegetation dynamics and associated animal diversity. Average annual precipitation increases east-west from the southwest SK border to the eastern ND border lying along the Red River Valley. Frost-free periods range from approximately 150 days in the southern region to less than 110 days in the boreal mixed-wood region of SK and MB. The great plains regions and prairie biomes experience high extremes in temperature, ranging as low as -45°C in January to as high as 40°C in July and August.

Western-most Distribution of *Parelaphostrongylus tenuis*

In order to achieve the first objective of this project, to determine the current western distribution of *P. tenuis* in WTD from SK, MB and ND, necropsy of WTD crania and recovery of adult *P. tenuis* were required. The presence of *P. tenuis* has been relatively well documented in WTD from the provinces and states of eastern North America (Figure 1, see review of Anderson and Prestwood 1981); however, *P. tenuis* distribution in SK, MB and ND was uncertain (Anderson and Prestwood 1981).

Bindernagel and Anderson (1972) established the western-most Canadian distribution of *P. tenuis* as SK based on the presence of dorsal-spined larvae in feces of WTD and necropsy of 121 WTD heads. An infected WTD collected from Virden, MB was the westernmost *P. tenuis* recovered during necropsy (*Ibid.*). Distribution of *P. tenuis* based on dorsal-spined larvae is an unreliable method to document presence of this parasite. Presence of a dorsal-spine on first-stage larvae, is a characteristic of six species of nematode found in North American ungulates. Three of these parasitic nematodes, *P. tenuis, Parelaphostrongylus andersoni* and *Varestrongylus alpenae* are found in WTD (Gray et al. 1985), indicating that a nematode other than *P. tenuis* could be represented by presence of dorsal-spined larvae. Thus, in an effort to verify the identity of dorsal spined larvae reported in feces of WTD from eastern SK, Gray et al. (1985) exposed captive WTD and mule deer to infective third stage larvae, from dorsal-spined first stage larvae recovered from WTD feces collected in SK. At necropsy, parasites recovered in experimentally infected deer were identified as *Varestrongylus alpenae*, a parasitic nematode of the lung of WTD. In 1972, when Bindernagel and Anderson published their *P. tenuis* distribution survey, the presence of *V. alpenae* in Canada was unknown and they falsely concluded that all dorsal spined larvae found in fecal samples were those of *P. tenuis*.

The discovery of *V. alpenae* in WTD of SK made the distribution of *P. tenuis* based on recovery of dorsal spined larvae unreliable, at least in northcentral North America. Therefore, the western boundary for *P. tenuis* needed to be redefined. Recovery of adult *P. tenuis* from the cranium of WTD was the only reliable method to establish the current western distribution of this parasite.

Prevalence and Intensity of *Parelaphostrongylus tenuis* in White-tailed deer

The second objective of this study was to examine relationships of deer sex, age class and density to prevalence (% of individuals infected) and intensity (number of parasites/ infected host) of *P. tenuis* infections. In free ranging WTD populations of eastern North America the prevalence of *P. tenuis* is highly variable (Table 2) and likely dependent on a combination of ecological factors. The association between prevalence and habitat type, land use, temperature, precipitation, presence of suitable intermediate hosts, soil type, WTD sex, WTD age, and WTD density remains unclear.

a) Association of Prevalence with Sex of White-tailed Deer

In surveys with prevalence determined separately for male and female WTD, some researchers report no significant difference between the sexes (Anderson 1963a, Behrend and Witter 1968 (in each individual age class), Behrend 1970, Garner and Porter 1991, Bogacyzk et al. 1993) while others have found prevalence to be higher in females than in males (Karns 1967, Behrend and Witter 1968 (($P < 0.05$) in females with all age classes combined), Prestwood and Smith 1969 (no test of significance), Gilbert 1973, Peterson and Lankester 1991, Jarvinen and Hedberg 1993).

b) Association of Prevalence with Age of White-tailed Deer

Prevalence has been shown to increase with deer age, suggesting that the longer an individual WTD shares range with WTD infected with *P. tenuis*, the more likely that the deer will come into contact with infective terrestrial snails and slugs, and in turn become infected with *P. tenuis* (Anderson 1963a, Karns 1967, Behrend and Witter 1968, Dew 1988, Garner and Porter 1991, Peterson and Lankester 1991).

c) Changes in Prevalence within a Deer Population through Time

As revealed in a number of studies, prevalence of *P. tenuis* in a WTD population is highly variable. In New York State prevalence in fawns fluctuated considerably from the mid 1960's to 1989; 36% Garner and Porter (1991), 42% Behrend (1970) and 64% Thurston and Strout (1978). Spatial variation in prevalence at a fine scale (*i.e.*, township, 9.6 x 9.6 km) is also highly variable (Prestwood and Smith 1969, Anderson and Prestwood 1981). This variability is likely a result of the presence of ecological "hotspots" for transmission (*i.e.*, *wet* creek bottoms or densely treed, deciduous dominated, forest areas), areas with ideal terrestrial gastropod habitat. These hotspots might be characterized by a moist organic litter layer, high densities of downed logs, abundant coarse woody debris, and abundant white-tailed deer forage on and near the forest floor (Clarke et al. 1968, Maze and Johnstone 1986).

The ability to compare changes in reported prevalence between studies is likely confounded by sampling intensity, age class distribution of WTD examined, time of specimen collection, method of diagnosis of infection (*i.e.*, Baermann technique *vs.* cranial necropsy), and necropsy technique (*i.e.*, whether or not cranial venous sinuses were searched). If a comparison of prevalence between studies is to be made, special attention must be paid to factors such as sample size and age class of WTD necropsied to ensure that the comparison is valid. Combining data between years and between age classes might ultimately influence the number of *P. tenuis* infections observed and thus the apparent prevalence reported.

d) Intensity of *Parelaphostrongylus tenuis* Infection in White-tailed Deer

Intensity of *P. tenuis* infections in WTD is relatively low, usually less than 5 *P. tenuis* / WTD. Of the 2409 deer examined from 74 counties in the southeastern US (Prestwood and Smith 1969), only seven counties reported a mean intensity greater than 5 *P. tenuis* / WTD, with a range of 1-120 worms recovered from a single deer. Of the 15 reports documenting intensity of natural infections of *P. tenuis*, not incorporated in the Prestwood and Smith review, only one documented a mean intensity greater than 5 (Table 3).

e) Influence of Ecological Variables on Prevalence

With respect to the third objective, to determine if the presence of *P. tenuis* was correlated to ecological variables, subjective path analysis was conducted based on what is known to date about the ecology of *P. tenuis* (Figure 2). The following parameters were selected as likely correlates to *P. tenuis* distribution and prevalence: temperature, precipitation, landuse, terrestrial gastropods, and WTD density. Past research has provided considerable information on the ecology and life cycle of *P. tenuis*, yet there are still many aspects of transmission, distribution, and host specificity of this parasite that remain unanswered.

To follow the logic behind why specific ecological variables were chosen over others, a review of the life cycle of *P. tenuis* is essential (Figure 3, see Anderson 1992). The life cycle involves two hosts, terrestrial gastropods, and WTD. Gravid female worms, in the cranium of WTD, pass eggs into blood vessels of the brain. Eggs then travel through the circulatory system and are filtered out of the blood as emboli in capillaries of the lungs. Here they develop into first stage larvae, which are carried up the bronchi via ciliary action and swallowed. Larvae pass down the digestive tract and are shed with the feces in the layer of mucous that coats the fecal pellets (Lankester and Anderson 1968). The larvae are probably readily rinsed from the feces into the soil by rain or melting snow (Lankester and Anderson 1968). Larvae actively penetrate the foot of the intermediate host (Platt and Samuel 1984), terrestrial gastropods, as the gastropods move either through the soil and litter layer or across contaminated deer feces.

First stage larvae are very resistant to a wide range of temperatures and relative humidity. Shostak and Samuel (1984) found that survival of first stage larvae of *Parelaphostrongylus odocoilei* (similar life cycle to *P. tenuis*) increased with decreasing temperature (20°C to -18°C) and decreased with repeated cycles of freezing and thawing. Desiccation also reduced the infectivity of first stage larvae of *P. odocoilei* for snails. Alberta-origin larvae of *P. odocoilei*, a muscle worm of mule deer, also proved to be more resistant to freezing than Pennsylvania origin larvae of *P. tenuis*. The influence of solar radiation has been suggested as an important factor affecting survival of nematode larvae (Senger 1964), but there are no data for first stage larvae of *P. tenuis*.

Upon entering a snail, larvae develop and molt into third-stage larvae that are infective to deer. Development from first stage larvae to third stage larvae within the intermediate host continues during summer as long as the snail is active; development stops in estivating snails (Lankester and Anderson 1968). Rate of development within terrestrial gastropods is associated with ambient temperature. Under constant temperatures of 20°C, first stage larvae developed into infective third stage larvae in 3-5 weeks (Peterson and Lankester 1991). In field conditions with continuously fluctuating temperatures, larval development may take considerably longer than 5 weeks. Previous research has indicated that larvae can successfully over-winter in terrestrial snails and slugs (Lankester and Anderson 1968).

Deer or other suitable hosts likely become infected by accidentally ingesting infected snails while grazing. Presumably the increased temperature inside the digestive tract of deer stimulates increased activity of third stage larvae, and the larvae penetrate the gut (abomasal wall) and enter the visceral cavity (Anderson and Strelive 1967). Once in the body cavity of the deer, larvae locate a peripheral nerve and migrate to the spinal cord. Larvae continue to develop, as they migrate along the subdural space to the cranium (Anderson and Prestwood 1981) where they mature and begin to shed eggs into the venous blood vessels. Mature adult *P. tenuis* are common in the cranial cavity and in the transverse, sagittal, and cavernous sinuses. About 3 months after an infected gastropod is ingested, first stage larvae appear in the feces.

f) Association of Climate with Prevalence

Precipitation and temperature may be significant climatic variables that influence both the distribution and prevalence of *P. tenuis* possibly by directly or indirectly affecting numbers of intermediate or definitive hosts, and survival of first stage larvae. Bindernagel and Anderson (1972) hypothesized that the grassland biome of the great plains region may, because of its low precipitation and high temperatures, act as a significant ecological barrier preventing the westward spread of *P. tenuis*. Behrend and Witter (1968) suggested that the influence of precipitation on the abundance and distribution of *P. tenuis* intermediate hosts (terrestrial snails and slugs) may be an important factor determining the distribution and abundance of *P. tenuis*. They commented that the wetter than normal year in Maine (1967) may have contributed to the high prevalence of *P. tenuis* (84%, n = 196); however, in a study in New York (Garner and Porter 1991), no such correlation between precipitation and *P. tenuis* prevalence was found.

In a 10 year study of the presence of *P. tenuis*-like first stage larvae in feces of WTD fawns and yearlings, Peterson and Lankester (1991) found that the year during which May through August was the driest in 12 years, coincided with the lowest reported prevalence of first stage larvae in the fawns of that year. The authors concluded that this dry year may have restricted transmission, thus resulting in the low prevalence in fawns of that year.

Recognizing that survival of first stage larvae, and distribution and abundance of terrestrial gastropods might be directly influenced by precipitation, the following hypothesis was presented: that during the time of year, spring, summer and fall, when precipitation might be a limiting factor, precipitation will be higher in deer management units (DMUs) with *P. tenuis* present than in deer management units where no *P. tenuis* was found.

In addition to total accumulated precipitation, frequency of precipitation might also have a significant effect on the transmission of *P. tenuis*. Entire monthly precipitation accumulated over light daily rain showers versus a single heavy downpour might have different consequences in terms of availability of first stage larvae. Even with the presence of dense overstorey vegetation, heavy downpours could rinse the larvae off fecal pellets and into the litter layer or small drainages, possibly decreasing their potential for transmission. Increased activity of snails and slugs might also depend on moist ground conditions (Locasciulli and Boag 1987) associated with frequent rains. Less frequent rains might result in decreased snail and slug activity thereby reducing transmission opportunities. I hypothesized that *P. tenuis* will be present in DMUs that receive rain most frequently during the likely transmission period, May through October.

Development of third stage larvae of *P. tenuis* within the gastropod host depends on activity of the gastropod, which in turn depends on ambient temperature (Lankester and Anderson 1968). Therefore, it was hypothesized that DMUs with *P. tenuis* present would have higher spring, summer, and fall temperatures than DMUs where *P. tenuis* was not found. Because temperature extremes may arrest development of third stage larvae in gastropods or could, if high enough, be lethal to first stage larvae or gastropods, I hypothesize that management units with *P. tenuis* absent will have the lowest or highest respective daily minimum or maximum temperatures.

Freezing, and repeated freezing and thawing substantially decreases survival and infectivity of first stage larvae of *P. tenuis* (Shostak and Samuel 1984). Snow accumulation, when deep enough, has excellent insulative properties and a temperature moderating effect at the snow-soil interface. If snow accumulation is greater than 20 cm, temperatures at the soil-snow interface remain relatively constant at 0°C (Halfpenny and Ozanne 1991). Therefore, areas with significant snow pack would have fewer dramatic temperature fluctuations over winter and fewer freeze/ thaw cycles at the snow/ soil interface than areas with little snowpack. This could potentially reduce mortality of first stage larvae thus increase infectivity of first stage larvae, and increase survival of over-wintering gastropods. Based on this reasoning I hypothesize that DMUs with *P. tenuis* present will receive higher amounts of snow than units where *P. tenuis* was not found.

Ambient temperature influences activity of terrestrial snails and slugs (Burch 1962). Snails and slugs in areas with more days above freezing might remain active longer, thus potentially increasing the length of exposure to gastropods (Peterson and Lankester 1991). I hypothesize that the number of days below freezing for May through October will be lower for DMUs with *P. tenuis* present than for DMUs with no *P. tenuis*.

g) Association of Gastropod Abundance and Distribution with *Parelaphostrongylus tenuis*.

There is a relatively high number of species of known intermediate hosts occurring within the eastern range of *P. tenuis*. Of the approximately 40 species of snails and 5 species of slugs examined, *P. tenuis* infections have been found in 14 species of snails and 4 species of slugs. Of the four major studies of intermediate hosts of *P. tenuis* (Lankester and Anderson 1968, Kearney and Gilbert 1978, Maze and Johnstone 1986 and Rowely et al. 1987), the slug, *Deroceras laeve*, tended to be the most abundant and commonly infected gastropod. *Deroceras laeve*, is an annual species that over-winters as an adult with the entire cohort dying after laying eggs in June and July. Other abundant intermediate hosts include *Zonitoides* *nitidus* and *Zonitoides arboreus*. *Zonitoides arboreus* and *Z. nitidus* live 2-3 years (Lankester and Anderson 1968).

h) Association of White-tailed Deer Density with Prevalence

Deer density has also been implicated as playing an important role in the transmission and prevalence of *P. tenuis*; however, qualitative data to support or refute this hypothesis have not been presented. In the North, WTD in the boreal mixed-wood forest are difficult to census, and density and abundance data are lacking for many regions. Game management units that do provide an estimate of deer density commonly express deer densities as deer/ km^2. These density calculations typically include unsuitable deer habitat (*i.e.*, areas of extensive cultivation and lakes); therefore the actual density of deer may be considerably greater than reported because deer are likely concentrated in fragments of suitable habitat.

Some anecdotal evidence has been published supporting the correlation of high deer density with high prevalence of *P. tenuis*. Prevalence of *P. tenuis* was higher in central Minnesota, where deer densities were reported to be greater than 30 deer/ $mile^2$ (~10 deer/ km^2), than in northern Minnesota where there were fewer deer (Karns 1967). Behrend and Witter (1968) suggested a positive relationship between deer density and *P. tenuis* in Maine where the prevalence of *P. tenuis* was highest where deer populations were presumably the densest and had been expanding. In contrast, Garner and Porter (1991) reported no correlation between deer density and prevalence in New York, but they did find a high prevalence of first stage larvae in feces of deer from a high density area (6.8 deer/ km^2). Lankester (1974) found no correlation between high deer density areas (2.5 deer/ km^2) and high prevalence of *P. tenuis* in southern MB; however, he stated that the deer density estimates used may have been misrepresentative because they included cleared agricultural land. Thomas and Dodds (1988) and Peterson and Lankester (1991) reported no correlation between deer density and prevalence in Nova Scotia and northern Minnesota, respectively.

II) METHODS

1) Collection and Storage of White-tailed Deer

Distribution, prevalence and intensity for MB, ND and SK was determined by examining crania of WTD for adult *P. tenuis*. Sampling protocol was designed to determine the current western-most distribution of *P. tenuis* based on sampling deer from as many deer management hunting units as possible. In 1989 deer heads were collected from wherever they were available within the three jurisdictions. In 1990, collection efforts focused on increasing the number of heads from management units with a sample size of less than 30 heads collected in 1989. Management units with 30 or more WTD heads collected in 1989 were not resampled in 1990. Heads from WTD killed in 1989 were necropsied in February through August, 1990; those collected in 1990 were necropsied in January through August, 1991.

Deer heads were collected in cooperation with state and provincial fish and wildlife departments. In advance of the annual November deer hunting season, arrangements were made with local wildlife enforcement branches, wildlife research agencies, local hunting clubs, and meat processing plants to collect as many deer heads as possible. Emphasis was placed on the importance of knowing where deer were killed, at least to deer management unit (Figures 4 - 6) and more precisely if desired. In ND, all WTD killed during the hunting season had to have the canceled hunting license attached to the carcass. This canceled hunting license had the date of kill, and Gun Hunting Unit recorded on the license. Deer collected from ND typically had the canceled license attached to the ear or around the base of an antler, if the tag was attached to the hock or through the hide, the tag was relocated to the head, or the head was retagged with a paper label recording all relevant information in indelible ink. In MB and SK, information on date of kill and location of kill (at least to resolution of DMU) for all deer heads was recorded by provincial game management personnel. Either the canceled hunting license or a paper label was attached to all WTD heads collected. Heads were stored in freezers or outside (cool or frozen) until retrieval and transport to Edmonton, Alberta.

Sex of individual WTD was determined by the presence or absence of antler pedicels on the frontal bones. All heads with pedicels present were classified as males.

In each of November 1989, January 1990, November 1990, and January 1991, a collection tour was made through SK, ND and MB. Heads were collected at designated pick-up points, loaded into a stock-trailer (18 ft), and transported back to the Alberta Fish and Wildlife Services' Provincial Laboratory in Edmonton. During winter, heads were stored outside at the University of Alberta, Ellerslie Research Farm and then, as spring approached or as room became available, heads were relocated to walk-in freezers at the University of Alberta (9 th floor, Department of Zoology) and Fish and Wildlife Services' Provincial Laboratory (7 th floor, O. S. Longman Building). After necropsy all heads were incinerated.

Through repeated handling, and during thawing of heads prior to necropsy, some labels or tags became illegible. If the state or province from where the WTD head originated from could not be discerned, the head was discarded. If game management unit could not be discerned, but source by province or state was known, the head was necropsied and included in the province or state summary.[1]

2) Necropsy

Frozen heads were sagittally sectioned using a heavy duty meat cutter's bandsaw. The sagittal cut through the cranium was offset approximately 3mm from the median plane to reduce the chance of destroying worms within the sagittal venous sinus. The thinnest possible blade (2 mm kerf) was utilized to minimize the risk of destroying worms during sectioning. After heads had thawed overnight, inspection for adult *P. tenuis* began. First, for each specimen, both sagittal sections were inspected along the surface of the cut. The cerebrum and cerebellum were carefully teased away from the meninges, and surfaces were visually inspected under bright light. Sulci were probed and each sagittal half of the brain was sectioned (~1 cm intervals) and examined for *P. tenuis* embedded in neural tissue. The olfactory bulb was then teased away from the cribiform plate using a scalpel and carefully examined for *P. tenuis*. With the neural tissue entirely removed from the cranium, the surface of the meninges was then examined using a dissecting microscope at 6x. Cavernous, transverse and sagittal sinuses were opened using a scalpel and forceps and examined at 6x. Location of any worms found were carefully mapped. The total number of worms for each

---

[1] Apparent discrepancy between total number of WTD necropsied when game management unit sample sizes are added, in comparison to sample sizes provided for provincial and state summaries, is due to inability to resolve from which deer management unit some heads originated.

head was recorded and all specimens fixed in a glycerin alcohol solution. All deer sampled were classified as adult, yearling, or fawn based on mandibular tooth eruption patterns (Severinghaus 1949). When an infected deer was discovered that could not be aged accurately based on tooth eruption pattern alone (n = 93), the first incisor was extracted, cleaned, sealed in a clearly marked envelope, and sent for sectioning, staining and mounting.[2] Mounted slides were then returned to the University of Alberta, Department of Zoology, and age was interpreted based on cementum annuli analysis (Matson 1981).[3]

For a number of heads, if all pertinent information was recorded with the exception of deer management unit or sex or age, the head was included in all possible analyses; *i.e.*, if the sex of the deer was not recorded the deer was excluded from all analysis examining *P. tenuis* relationships with deer sex.

To determine whether or not a significant difference existed between groups, Chi Square analysis was conducted. A statistical significance level of $P < 0.05$ was used for all tests unless stated otherwise (Sokal and Rolf 1989).

Any future reference to deer shall mean WTD unless stated otherwise.

3) Climate

The finest spatial scale in which distribution and prevalence of *P. tenuis* could be resolved was deer management unit: Game Management Zones in SK (Figure 4), Game Hunting Areas in MB (Figure 5), and Deer Gun Hunting Units in ND (Figure 6). Because several of these DMUs contained more than one weather station, while others did not have a single weather station (Anonymous 1989a,b), an effort was made to select a weather station that was most representative of the biogeoclimatic features (*i.e.*, latitude, longitude, elevation, slope, aspect) of that DMU. In MB, 29 of 169 climate stations were selected to represent the 35 Gun Hunting Areas (Appendix IA). In ND, 31 of the 149 state-wide climate stations were selected to represent the 38 Gun Hunting Units (Appendix IB). In SK, 43 of the 286 province-wide climate stations were selected to represent 50 Wildlife Management Zones (Appendix IC).

---

[2] Matson's Laboratory, P. O. Box 308, 8140 Flagler Road, Milltown, Montana 59851

[3] Blind controls - 2 incisor roots (I1) from the same deer were sectioned, stained and labeled. Age of each sample was determined without knowledge that the stained sections were from the same deer. Age determination based on each stained section from the same deer were then compared as a measure of precision.

Climate data for ND were analyzed separately from the climate data for MB and SK. Preliminary analysis between ND, and MB and SK revealed that the associated change in latitude had a significant effect on seasonal temperatures and seasonal precipitation. In order to minimize dilution of these discrete differences, and avoid confounding effects pooling climate data between jurisdictions may have on interpretation of the results, analysis of climate data between jurisdictions was kept separate. Further justification for keeping MB and SK climate data separate from ND data was due to different methods of data collection, data storage, and variability in number of years that data were recorded.

Climatological data for ND for 1989 and 1990 were obtained from the National Climatic Data Center, Asheville, North Carolina (Anonymous 1989, 1990). All climatological data obtained for ND were collected and stored in English units. A simple computer program was written to convert all values to metric measures. Climatological data for MB and SK were obtained from Environment Canada, Atmospheric Environment Service. Normals data[4] were determined using the 30 year mean (1951-1980) (Anonymous 1980). The following information was used to determine ecological associations between climate and presence and prevalence of *P. tenuis* :

a) average daily, monthly, seasonal, and annual precipitation,

b) average daily, monthly, seasonal, and annual temperature,

c) monthly maximum, minimum, and average temperatures,

d) number of days > 0°C/ month, and

e) number of days precipitation/ month.

3a) Association of Climate with Distribution and Prevalence

Because WTD necropsied for this project were collected over a 2 year period, prevalence data for *P. tenuis* was compared with climate data on two temporal scales: 1) long-term, referring to climate normals and 2) short-term referring to annual climate. The long term, climate normals data is simply the 30 year average climate for a given area. For climate normals to be correlated with the presence or absence of *P. tenuis* I made the assumption that:

---

[4] Future reference to normals data refers to 30 year mean (1951-1980) unless stated otherwise.

1) prevalence of *P. tenuis* in a deer population does not fluctuate markedly year to year over short time periods (*i.e.,* ≤ 2 years)

2) annual fluctuation in climate does not have a great effect on prevalence of *P. tenuis* within the deer population as a whole, but rather long term "normal" ecological conditions are what determine presence/ absence and prevalence of *P. tenuis.* Accepting these two assumptions, I pooled prevalence data (age and sex combined) for all DMUs between years and compared prevalence with the normals data.

All DMUs sampled in MB, SK, and ND were grouped according to whether or not *P. tenuis* was present or absent.

The following parameters were used to test for correlation with the presence of *P. tenuis* within each DMU sampled from ND (n = 31), and MB and SK (n = 75):

1) Mean Normal Annual Temperature

2) Mean Seasonal Temperature

3) Monthly Average Maximum Daily Temperature

4) Monthly Average Minimum Daily Temperature

5) Monthly Average Mean Daily Temperature

6) Number of days/ month below freezing (ND only)

7) Mean Normal Annual Precipitation

8) Mean Seasonal Precipitation

9) Mean Normal Monthly Rainfall

10) Mean Normal Monthly Snow and Sleet

11) Mean Normal Monthly Precipitation

12) Normal Number of Days Rain (MB/SK only)

13) Normal Number of Days Snow (MB/SK only)

14) Normal Number days Precipitation

Mean values for each of the 14 previously listed parameters, for all 106 DMUs sampled were determined for each month (except for annual summaries). Mean values (and standard errors) for DMUs with *P. tenuis* present were compared with mean values (and standard errors) for units with *P. tenuis* absent using a paired-sample t test (Zar 1984). A significance level of $P < 0.004$ was used to determine whether or not monthly means differed significantly between units with *P. tenuis* compared to units without. This P value was selected to ensure that differences between means were in fact highly significant.

Correlation of *P. tenuis* with the ecological variables was tested further using univariate and multivariate nominal logistic regression models (SAS Institute Inc., 1989). Logistic regression models were used to determine the association of each ecological variable with the presence or absence of *P. tenuis*, as well as determine which combinations of ecological variables were most strongly correlated with the presence of *P. tenuis*. For variables with a significant correlation to presence of *P. tenuis*, an attempt was made to define threshold values describing the probability of having *P. tenuis* present under specific ecological conditions.

Univariate linear regression analysis was conducted to determine whether or not increasing prevalence of *P. tenuis* was correlated with monthly and seasonal temperature, and monthly and seasonal precipitation. Only DMUs with a sample size greater than one and with *P. tenuis* were included in this analysis ($n = 27$).

3b) Association of Annual Climate with Distribution and Prevalence of *Parelaphostrongylus tenuis*.

Annual climate was the second temporal scale used to determine ecological variables associated with the presence or absence of *P. tenuis*. For annual climate to have a correlation with presence of *P. tenuis*, I made two assumptions:

1) presence or absence of *P. tenuis* may change over short periods of time (*i.e.*, ≤ 2 years),

2) prevalence, especially prevalence in fawns, may fluctuate annually depending on transmission conditions and number of immunologically naive hosts (no prior exposure to nematode parasites).

If *P. tenuis* transmission was sensitive to annual climate change, then this change in transmissibility should manifest itself as a change from year to year in the prevalence of *P. tenuis*. Changes in prevalence in fawns would be the best indicator of transmission conditions for that season; however, because the sample size for this study was designed to determine distribution only, sampling intensity of fawns within the same DMU for each of 1989 and 1990 was not large enough to allow a rigorous statistical test of the correlation of prevalence in fawns with annual climate. In an attempt to test if this association with annual climate and annual prevalence did exist, and in the absence of an adequate fawn sample, prevalence data was pooled for fawns, yearlings, and adults.

At a geographic scale broader than DMUs, prevalence for fawns in each of two regions, southeastern MB and eastern ND, was pooled. Annual prevalence data were then compared to the respective annual climate data (*i.e.*, each management unit, 1989 prevalence compared with 1989 monthly and seasonal temperature, and monthly and seasonal precipitation). The objective was to determine whether or not annual changes in prevalence were correlated with annual fluctuations in climate.

Statistical analysis involved univariate linear regression analysis between *P. tenuis* prevalence and climate variables of temperature and precipitation.

4) Association of Gastropod Intermediate Hosts with Distribution and Prevalence of *Parelaphostrongylus tenuis*

To determine distribution and relative abundance of intermediate hosts of *P. tenuis*, terrestrial gastropods were collected at 11 sites (MB n = 5, SK n = 6) running East - West, from the southwest corner of SK (Battle Creek) to the southeast corner of MB (Moose Lake), and along 6 sites (MB n = 3, ND n = 3) running South-North along the North Dakota-Minnesota border, from ~200km south of the Canada-United States border, to ~300km (Gypsumville, MB) north of the Canada-United States border. Gastropods were collected from July 10 to July 22, 1991. Collection sites were located approximately every 75 km along each transect. Snails were trapped using 30 cm x 30 cm pieces of brown corrugated cardboard soaked in pond water and laid flat on the ground. To prevent cardboard from drying, 50 cm x 50 cm, black, 4 mm polythene was centered over each tile and pegged in place with small stakes. Sites were chosen such that they represented the most suitable terrestrial gastropod habitat. All sites were vegetated with shrubs or trees > 60 cm in height and shaded from direct sunlight from late morning to nightfall. Once a site-center was selected, a random compass bearing was taken and cardboard pieces were placed every 5 m along a 50 m transect. Midway along the transect a shallow soil pit was excavated, thickness of litter layer was noted, and soil was classified as either sand, clay, or organic. Cardboards were left in place ~48hrs; after the second night that a piece of cardboard had been placed, each was retrieved early in the morning (28 mins prior to sunrise - ~3 hrs after sunrise). All slugs on the cardboard were counted and all snails were collected and transported back to the University of Alberta for identification. In addition to the 17 sites located in deer feeding areas (confirmed by tracks, pellet groups, and foraging activity), three additional sites were selected to determine the presence and abundance of terrestrial gastropods in what was subjectively described as sub-optimal terrestrial gastropod habitat. Sub-optimal Site 1 (Sandilands, MB) was a jackpine (*Pinus banksiana*) dominated forest characterized by sandy soil, shallow litter layer, and greatly reduced understorey vegetation. Sub-optimal Site 2 (Conway, ND) was located in a windbreak ~12 m wide dominated by elm (*Ulmus* spp.) > 18 m in height, both sides of this windbreak were surrounded by row crops of potato. Sub-optimal Site 3 (Buxton, ND was another windbreak dominated by elm with a honey suckle (*Lonicera* spp.) understorey, both sides of the 8 m wide windbreak were surrounded by row crops of potato. Sampling protocol at these suboptimal sites was identical to the other 17 sites except if low numbers of gastropods were recovered on the cardboard, an intensive physical search of the litter layer and beneath downed logs was conducted.

An accurate numerical assessment of abundance of gastropods for the 20 sites was not possible due to the influence of temperature change and variable precipitation throughout the trapping period. Population estimates of terrestrial gastropods are confounded by the high variance in the number of gastropods recovered at any one trapping period (Boag 1990). Prior to initiation of the gastropod survey an experiment was conducted in Edmonton, Alberta to assess the validity of abundance estimates using the cardboard trapping method described above. Abundance of snails and slugs recovered on the cardboard varied unpredictably with ambient temperature, humidity, and time of day cardboard was recovered. However, repeated surveys of the same area revealed that the number of species trapped was most consistent when cardboard remained damp, cardboard was undisturbed, and cardboard was recovered during cooler daytime temperatures associated with early morning. The number of individuals of all gastropod species recovered on the cardboard at each site were recorded.

Gastropods were identified based on shell morphology using descriptions in Burch (1962) and Pilsbry (1948) and comparison with known snails in the Department of Zoology collection at the University of Alberta.

5) Association of White-tailed Deer Density with Distribution and Abundance *Parelaphostrongylus tenuis*

Data on WTD density were obtained from provincial and state wildlife management agencies (MB Fish and Wildlife, ND Game and Fish, and SK Environment and Resource Management Dept.) and standardized as deer/square kilometer of land. Data could not be obtained for all DMUs; therefore, only units with density information were included in analysis. All agencies admitted that the precision of their deer density estimates were questionable and only SK was able to provide confidence limits for the few management units (20 of 76) in which they conducted aerial surveys for WTD (D. Brewster pers. comm.). Because of the low confidence limits on the density estimates provided, deer density was pooled from numerical estimates into three categorical values: low (0 - 0.37), medium (0.37 - 1.1), and high (>1.1 WTD/ km^2). Deer density was then compared to presence or absence of *P. tenuis* using univariate logistic regression analysis.

6) Association of Elevation and Forest Cover with Distribution and Abundance of *Parelaphostrongylus tenuis*

Land use information, specifically percentage of DMU forested, was determined from computer interpretation of Landsat satellite color photograph interpretation supplemented with infrared high-elevation aerial photograph interpretation, and Land Cover Associations (The National Atlas of Canada, 5th Edition, Energy, Mines and Resources Canada, 1989). Because of difficulty discerning shrub types from 1) early successional forest types, 2) late season cultivated crops, and 3) grazed forest lands, and from difficulty obtaining digital land coverage data, percentage of each deer management unit forested was expressed as categorical vs. numerical data. Four categories were established: < 25%, < 50%, <75%, and <100% forested[5]. Each DMU examined for *P. tenuis* was then assigned a category.

Elevation of each DMU was assigned by selection of a climate station that was representative of the entire DMU and then extrapolating the elevation of that climate station to the entire DMU. Elevation was then compared to the presence or absence of *P. tenuis* using univariate logistic regression analysis.

[5] %forested refers to natural stands of timber >15m height (excludes shelter belts)

III) RESULTS

1) Distribution and Prevalence of *Parelaphostrongylus tenuis*

Of the 2186 deer collected in 1989 and 1990, 1902 were examined for *P. tenuis* (213 were discarded due to unknown origin and 71 were discarded due to severe cerebral hemorrhage, advanced stage of decay, or incomplete data). Overall prevalence for all heads necropsied was 10.3%; almost all infected deer were from ND and MB (Table 4). Infected deer were found in eastern ND (Figure 7), southern MB (Figure 8), and southeastern SK (Figure 9). The highest prevalence of *P. tenuis* was in southeast MB; prevalence decreased with increasing distance northwest, west, and southwest of this region (Figure 10).

2) Association of Sex of White-tailed Deer with Prevalence of *Parelaphostrongylus tenuis*

There was no significant difference in prevalence between sexes for all deer examined (104 of 984 male deer infected, 90 of 916 female deer infected). Subdivision of the data into provincial or state jurisdiction also revealed no significant difference between sexes [ND: ($DF = 1$, $X^2 = 3.34$, $P < 0.068$); MB: ($DF = 1$, $X^2 = 0.46$, $P < 0.50$)]. In ND, prevalence in males and female deer was 5.7% and 10.1% respectively. In MB, prevalence in male and female deer was 18.9% and 18.0% respectively (Table 5). Further subdivision of the samples by age class, within each jurisdiction, again revealed no significant difference in prevalence between sexes within each age class ($P > 0.05$) (Table 6).

3) Association of Age of White-tailed Deer with Prevalence of *Parelaphostrongylus tenuis*

There was a significant difference in prevalence of *P. tenuis* between age classes with prevalence increasing through fawn, yearling, and adult deer age class (Table 7). For all years combined, differences in prevalence between age classes were significant for ND ($DF = 2$, $X^2 = 9.69$, $P < 0.011$) and MB ($DF = 2$, $X^2 = 12.72$, $P < 0.0043$) but not SK. When the samples were subdivided by year of kill, increased prevalence with increased age class was not always significant. In ND, in 1989, there was no significant difference in prevalence of *P. tenuis*, between age classes. In 1990, prevalence ranged from 6.1% in fawns (n = 66) to 9.9% in yearlings (n = 81), to 20.9% in adults (n = 91) (DF = 2, $X^2 = 8.49$, $P < 0.025$). However, when a significance level of $P < 0.10$ was used the difference between age class was again significant.

In MB, in 1989, prevalence in fawns, yearlings, and adults was 9.5, 18.5 and 21.4%, respectively (DF = 2, $X^2 = 8.38$, $P < 0.025$), and in 1990 prevalence was 11.4, 19.0 and 26.9%, respectively (DF = 2, $^2 = 8.47$, $P < 0.025$).

4) Association of Age of White-tailed Deer with Intensity of *Parelaphostrongylus tenuis* Infections

Numbers of worms present were recorded in 187 of the 195 infected deer. Mean intensity of infection was 2.3 (± 1.8 S.D.). The highest number of worms/ deer was 11, which were recovered from two individual deer. Single worms were recovered from 44.6% (n = 83) of the infected WTD and 67.2% (n = 125) had two or fewer worms (Figure 11).

There was no significant difference between intensity of infection in fawns, yearlings, and adults. Similarly there was no difference in mean intensity for the 155 infected deer, where exact age was known and where number of worms present were determined (Figure 12).

In ND, mean intensity of infection for 45 infected deer was 2.10 (± 1.65 S.D.). For all infected deer from the 1989 ND samples (n = 29), the highest intensity was nine worms, recovered from only one female fawn. Of the 29 infected deer, 19 (66%) had two or less worms. For the 13 infected deer from the 1990 ND samples, the highest intensity was four worms, recovered from an adult female deer. In ND, in 1990, mean intensity of infection in yearlings and adults was 1.8, and 2.3 respectively, with nine (69%) of the 13 infected deer having two or less worms. Only one infected fawn was observed in the 1990 samples and this deer had two worms.

In MB, mean intensity of infection of *P. tenuis* reported from 145 infected deer[6] was 2.2 (± 1.5 S.D.). In MB, of the 108 infected deer collected in 1989, the highest intensity was 11 worms, recovered from an adult male. Mean intensity of infection in fawns, yearlings, and adults was 1.6, 2.2 and 2.4,

[6] Total number of infected deer from MB was 149; however, exact number of worms could not be determined for four heads.

respectively. Of the deer collected in 1989, 67% had two or less worms recovered during necropsy. In 1990, for the 35 infected deer from MB[7], highest observed intensity of infection was 11, recovered from two deer, a yearling male and an adult male. Mean intensity of infection in fawns, yearlings, and adults was 2.0, 1.8 and 2.6, respectively. Of the 35 infected deer, 69% had two or less worms.

In SK, the single infected deer was an adult female, and only one adult worm was recovered (Table 8).

5) Association of Climate Normals with Distribution and Prevalence of *Parelaphostrongylus tenuis*

Throughout the study area, normal regional temperatures for each DMU did not appear to have any correlation with the presence or absence of *P. tenuis*. Using a paired t-test on the means, no significant difference (Appendix IIA-B) was found between normal annual temperature (Figure 13), or seasonal temperature (Figure 14) in DMUs with *P. tenuis* present compared to DMUs with *P. tenuis* absent. Also, monthly means of daily maximum, daily minimum, and daily average temperature were not significantly different for DMUs with or without *P. tenuis* (Figures 15 - 16). In ND, an index of freeze-thaw periods, measured as the number of days below freezing each month, was tested for correlation to DMUs with, and DMUs without, *P. tenuis*; there were no significant differences (Figure 17).

Throughout the study area, annual precipitation was significantly higher in DMUs with *P. tenuis* present than DMUs with *P. tenuis* absent (Figure 18). Seasonal precipitation, particularly during the latter part of the growing season, summer through fall, was also higher in DMUs with *P. tenuis* present (figure 19).

In ND and MB/ SK, during the later part of the growing season, total monthly precipitation (rain, sleet, and snow) was higher in DMUs with *P. tenuis* present. In ND, precipitation was significantly higher in August through October for units with *P. tenuis* present. In MB and SK, precipitation was significantly higher for DMUs with *P. tenuis* present, for August through November. Thus, Mb and SK

---

[7] Total infected deer from MB in 1989 and 1990 was 143/ 145 as two infected deer were collected outside this two year period.

DMUs with *P. tenuis* had one additional month/ year when precipitation was significantly higher compared to DMUs in ND with *P. tenuis* (Figure 20).

Not surprisingly, with the significant trend associated with total precipitation, higher monthly rainfall was also strongly correlated with the presence of *P. tenuis* in DMUs. In ND, monthly rainfall was significantly higher in DMUs with *P. tenuis* from August through October, and in MB and SK, rainfall was significantly higher from August through November. Compared to ND, MB and SK DMUs with *P. tenuis* present had higher rainfall for one month longer in the fall (November), for an annual effect of one more month/ year of higher rainfall than in ND (Figure 21).

Throughout the study area, precipitation in the form of snow and/ or sleet was not significantly different between DMUs (Figure 22).

Frequency of precipitation (number of days of rain, sleet, or snow each month) did not seem to be as highly correlated with the presence of *P. tenuis* as was amount of precipitation. In ND, no significant difference in days of precipitation/ month was found between DMUs with *P. tenuis* compared to DMUs without. In MB and SK, for September through November, days with precipitation were significantly higher for DMUs with *P. tenuis* compared to DMUs without (Figure 23).

In MB and SK, a comparison of the number of days with rain, sleet, or snow each month revealed that frequency of rain was significantly higher for DMUs with *P. tenuis* compared to DMUs without, for October through November. The number of days with snow, however, was not significantly different for DMUs with *P. tenuis* present compared to DMUs with *P. tenuis* absent (Figures 24).

6) Association of Annual Climate Conditions with Distribution and Prevalence of *Parelaphostrongylus tenuis*

Correlation of presence/absence of *P. tenuis* with annual climate was done using logistic regression analysis. In ND, only one significant difference between DMUs with *P. tenuis*, compared to DMUs without *P. tenuis*, was noted (Appendix IIB). This minimal correlation detected in comparing annual climate with presence/absence of *P. tenuis* in ND indicated that further analysis of annual means, using the MB/SK data and its associated lower resolution climate data (fewer climate stations over broader geographic areas) would be pointless.

To eliminate potential confounding effects of including adult deer in the analysis, one further test of the correlation of annual climate with the presence/absence of *P. tenuis* was conducted by selecting fawns from the data, determining prevalence for combined DMUs to increase sample size, and then comparing prevalence in fawns with regional annual climate data.

The pooled prevalence for all fawns from south-eastern MB was 9.5% (11/116) and 11.4% (4/35) for 1989 and 1990, respectively. Although not significant ($P > 0.05$), this apparent increase of prevalence in fawns of 1.9% was correlated with an increase in winter, spring, and summer precipitation in 1990 (January, February, March, April, May, June, and July). Of the seven management units for both 1989 and 1990 that had a sample of fawns and corresponding monthly precipitation data, there was higher precipitation at each station (12%-25% more) in 1990 compared to 1989.

The pooled prevalence for all fawns examined from eastern ND was 6.1% (4/66) and 1.6% (1/62) in 1989 and 1990, respectively. Although not significant ($P > 0.05$), this decrease in prevalence in fawns of 4.5% in 1990, was correlated with a hotter drier spring and summer (precipitation was 80% of normal, temperature was 1.7°C above normal).

7) Association of Gastropod Intermediate Hosts with Distribution of *Parelaphostrongylus tenuis*

A total of 619 terrestrial gastropods representing 15 species, five of which are known intermediate hosts for *P. tenuis*, were collected (Table 9). From all the sites sampled, ND had the highest mean number of suitable intermediate hosts followed by MB, and SK (Figure 25). Gastropods were most abundant in deciduous forested habitats with a dense tree canopy, moist litter layer, Luvisolic and Chernozemic soils, and abundant coarse woody debris and downed logs scattered on the forest floor. For all of the six trapping sites in SK, the mean number of species of known suitable intermediate hosts of *P. tenuis* recovered was 1.7 (range 1-3). Within SK, the highest number of species of suitable intermediate hosts recovered were associated with the increased abundance of aspen groves and treed draws found in the southeastern corner of the province (Gainsbourough Creek). Of the five sites in MB comprising the remainder of the West-East transect and the three sites comprising a portion of the South-North transect, the mean number of species of intermediate hosts recovered was 3.2 (range 1-4). The sites in MB with the greatest species richness and relative abundance of gastropods were associated with dense deciduous mixedwood forest with a heavy shrub understorey. In ND, of the four sites comprising the southern portion of the North-South transect, the mean number of species of suitable intermediate hosts was 3.7 (range 3-4).

8) Association of White-tailed Deer Density with Distribution and Prevalence of *Parelaphostrongylus tenuis*

Deer density was significantly correlated with the presence of *P. tenuis*. With the inclusion of all DMU' sampled, the r^2 value for predicting the presence of *P. tenuis* based on deer density alone was 0.12 ($P < 0.001$) with *P. tenuis* least likely to be present in units with low deer density. In areas of high deer density, the logistic regression model predicted that the probability of having *P. tenuis* present in the deer population was approximately 70% (Figure 26).

9) Association of Forested Land with Distribution and Prevalence of *Parelaphostrongylus tenuis*

Presence of *P. tenuis* was also correlated with forested land. Univariate logistic regression analysis was done on percentage of forested land Vs presence or absence of *P. tenuis* for all DMUs sampled. As predicted by forest cover alone, the absence of *P. tenuis* was most likely in DMUs with < 25% of the land area forested and *P. tenuis* was most likely present in DMUs > 25% and < 75% forested ($r^2 = 0.22$). In DMUs with between 50 and 75% forest cover, the forest class most likely to have infected deer, the model predicted a 70% chance that *P. tenuis* will be present in the deer population (Figure 27).

10) Association of Elevation with Distribution and Prevalence of *Parelaphostrongylus tenuis*

Throughout the study area, most DMUs with *P. tenuis* present occurred at significantly lower elevation than DMUs with *P. tenuis* absent. In ND, of the 31 DMUs sampled, units with *P. tenuis* present had a significantly lower mean elevation (370 m above sea level (ASL)) than DMUs with *P. tenuis* absent (610m ASL). In MB and SK, the mean elevation of units with *P. tenuis* present was 300m ASL and the mean elevation of units with *P. tenuis* absent was 507m ASL (Figure 28).

11) Correlation of Ecological Variables with Distribution and Prevalence of *Parelaphostrongylus tenuis*

a) Logistic Regression Models

For all DMUs sampled, mean monthly precipitation from March through November and mean monthly temperature from December through February generated significant univariate logistic regression models ($P < 0.05$). As mean monthly precipitation increased, the probability of having *P. tenuis* present within a deer population also increased. Mean monthly temperature for December through February and mean seasonal temperature for winter and spring, was inversely associated with the presence of *P. tenuis*; DMUs with lower mean temperatures had a higher probability of having *P. tenuis* present within the deer population. All r^2 values for significant climatic variables only, generated by the logistic regression models, are listed in Table 10.

Deer density, percent forested land, summer and fall precipitation, winter and spring temperature, and elevation generated a multiple logistic regression model that explained 58% of the variation in presence or absence of *P. tenuis* ($P < 0.001$). Of all the ecological variables analyzed, the seven mentioned above generated statistically significant models and had the highest predictability for the presence or absence of *P. tenuis*. Each of the five variables were forward and reverse loaded into stepwise logistic regression analysis. Summer precipitation had the single highest contribution followed by percent of DMU forested (Table 11). The multiple regression model generated indicated that the following were the specific conditions within the study area that had the highest correlation with the presence of *P. tenuis*: high summer and fall precipitation, cold winter and spring temperature, forest cover between 50 and 75%, high deer density, and low elevation.

b) Linear Regression Models

Linear regression analysis, including all DMUs within the study area with *P. tenuis* present, revealed no significant correlation between prevalence of *P. tenuis* infections and precipitation or temperature. When ND and MB data were analyzed separately significant correlations were found for ND only. In ND, winter and fall precipitation was positively correlated with prevalence (Figure 29). Linear regression analysis revealed a significant positive correlation between elevation of DMUs and winter temperature ($r^2 = 0.43$, $P < 0.001$).

DISCUSSION

The western and northern-most distribution of *P. tenuis* in north-central North America, originally defined by Bindernagel and Anderson in 1972, can now be clarified. The current finding of only one infected deer in eastern SK (only 60 km west of the MB border), and only one infected deer in western ND define the northwestern limit of *P. tenuis*. Whether or not these western-most infected deer indicate that *P. tenuis* is established in SK and western ND remains uncertain. It is possible that these western-most infected deer immigrated from the east to be killed in an area where, due to ecological factors, *P. tenuis* could not become established.

The dispersal ability of WTD suggests that the westernmost distribution of *P. tenuis* should be defined as a zone rather than as a discrete line. WTD in central North America typically have small home ranges (Carlsen and Farmes 1957, Nixon et al. 1991) and relatively short dispersal distances. Nixon et al. (1991) found that even in a highly fragmented agricultural landscape in Illinois, dispersal distances of females and fawns were less than 50 km. However, WTD are capable of long distance dispersal in excess of 230 km (Sparrowe and Springer 1970). Dispersing juvenile deer, especially males, are most likely to undergo long distance movements (Hawkins et al. 1971).

The fact that the two westernmost infected deer reported in this study were adult females suggests the possibility that they were resident deer, with home ranges within the DMUs in which they were killed.

Thus, new western most locations for *P. tenuis* are reported but whether or not the parasite is established in these locations is not known. For now the western limit of *P. tenuis* is defined as a zone of low prevalence, rather than as a discrete line, where *P. tenuis* may or may not be present in any given year.

Detection of *P. tenuis* along its western most boundary requires high sample size to detect the low prevalences that are associated with the western limits of this parasites range; *i.e.*, to detect a prevalence of 1% requires a sample size of at least 100 (Healy 1987, Gregory and Blackburn 1991). Past studies attempting to define the range of *P. tenuis* have typically used sample sizes too small to detect low prevalences (Sokal and Rolf 1980). Bindernagel and Anderson (1972) examined 60 heads from SK and 61 heads from MB. In Oklahoma, Kocan et al. (1982) conducted a state-wide survey in which 190 WTD heads were examined for *P. tenuis*. As in the study of Bindernagel and Anderson (1972), the sampling intensity in the western part of Oklahoma was potentially too low to detect low prevalence of *P. tenuis*. Similarly, Samuel (1969) found no *P. tenuis* in heads of 56 WTD from the Welder Wildlife Foundation Refuge in south Texas. Samuel and Holmes (1974) examined 140 WTD from Alberta for *P. tenuis*, and Foryet and Compton (1991) examined 95 WTD from Idaho; no *P. tenuis* was found. Again, the sampling intensity reported in these studies could have been too low to detect *P. tenuis* at low prevalences if it was present in these areas.

Whether or not the gradual decrease in prevalence of *P. tenuis* from the southeast corner of MB (>60%) west to the 100 th meridian (north-south line along the ND - Montana border) represents a prevalence distribution associated with an organism expanding its range, or the distribution of an organism restricted at the edge of its range by ecological factors, must still be considered. Bindernagel and Anderson (1972) hypothesized that the grassland biome of central North America may act as an ecological barrier to the western spread of *P. tenuis*. This hypothesis seems logical assuming that the hotter summer temperatures and lower precipitation in this biome (Anonyomous 1980) likely restricts activity, abundance, and distribution of the terrestrial snails and slugs that are the intermediate hosts of *P. tenuis*.

When Bindernagel and Anderson (1972) reported the distribution of *P. tenuis* in MB and SK, their results were based on examination of deer feces for presence of first stage larvae and necropsy of 121 deer heads. Thus, although they found adult *P. tenuis* in a WTD from as far west as near Virden, MB (50 km east of the SK border), they implied the presence of this parasite, based on presence of dorsal-spined first stage larvae in feces (9% of 364 pellet groups), virtually across all of southern SK. The discovery of the lungworm *Varelaphostrongylus alpenae* in WTD of eastern SK, with dorsal spined first stage larvae indistinguishable from those of *P. tenuis* (Gray et al. 1985), revealed that the westernmost distribution of *P. tenuis* reported by Bindernagel and Anderson was likely confounded by the presence of this then unknown parasite, *Varelaphostrongylus alpenae*. The present study, which relied on recovery of adult *P. tenuis*, makes the redefined western-most distribution of *P. tenuis* irrefutable.

The large sample size of this study provided statistical power for testing many of the discrepancies reported in the literature with respect to associations of WTD sex and age with *P. tenuis* intensity and prevalence. In this study, increasing prevalence with increasing age class from fawns through to adults was observed, this relationship is as one would expect, because the odds of a deer becoming infected increase with the length of time exposed to the parasite. The observation of this increase in prevalence with increased age indicates that exposure rates within the study area are not so high as to ensure that most WTD are exposed in one transmission season (June through November) as indicated for fawns in Minnesota (Slomke et al. 1995). If this were the case then prevalence in fawns would be the same as all other age classes.

Intensity of infection for WTD within the study area was lower (mean = 2.2 ± 1.50 S.D. for deer 0.5 - 10.5 years) than that reported recently for WTD in nearby Minnesota. These low parasite burdens in WTD may be due to a number of reasons. Low intensity in WTD could be due to low exposure to infective larvae. Past studies examining *P. tenuis* infections in gastropods revealed that intensity of infection, and prevalence in gastropods is very low (Kearney and Gilbert 1978, Maze and Johnstone 1986, Platt 1989) Infection of a WTD would require ingestion of many gastropods before an infected gastropod (with infective-stage larvae) is encountered. Also any infected gastropods that are ingested likely contain very few larvae (Lankester and Anderson 1968). As observed in this study, the lack of a significant difference between intensity of *P. tenuis* infections and deer age has two possible explanations. The first and most likely possibility is that, after initial exposure to typically few infective larvae, WTD develop an immune resistance to challenge infection. Given the suspected long life span of *P. tenuis*, old deer (i.e., > 8 years) may have acquired the infection as fawns and remained infective throughout their life without acquiring additional parasites by re-exposure to infective larvae. A second possible reason for the low intensity of infection is that *P. tenuis* is relatively short-lived within the WTD, possibly due to elimination of established adults by a successful immune response of the deer. In this case intensity of infection is maintained by continual recruitment of new parasites and immunological elimination of established parasites. This latter possibility seems less likely because most adult *P. tenuis* are able to evade the host immune response by residing within the immune-privileged subdural space associated with the central nervous system.

No significant difference in prevalence between males and females was documented. It had been suggested that behavioral differences between sexes may predispose one sex to higher exposure of infective gastropods resulting in differences in prevalence (Gilbert 1973). The lack of any significant difference in prevalence between sexes indicates that at the broad geographic scale used in this study, no predisposure of one sex to infected gastropods was detectable. Individual habits related to feeding behavior are likely more important in determining which individuals become infected. For example, deer that fed exclusively in cultivated crops, areas typically devoid of terrestrial gastropods, would be less likely to be infected than deer that fed exclusively on legumes near the ground beneath a forest canopy. Certain circumstances such as high hunting pressure may force behavioral changes that result in males foraging in areas with higher probability of ingesting infective gastropods. Given the behavioral plasticity of individual WTD, it seems unlikely that a significant difference in prevalence would be detectable unless behavioral differences between sexes could be confirmed, and that these behavioral differences would subject males or females to higher ingestion rates of infective gastropods.

In this study presence and prevalence of *P. tenuis* was significantly associated with ecological variables, especially precipitation and temperature. The variables found to be significantly associated with the presence of *P. tenuis*; (i.e., higher spring through fall precipitation, colder winter and spring temperatures, higher deer density, moderately forested areas, and low elevation) based on the hypothesized ecological requirements for successful transmission of *P. tenuis*, have a logical explanation. Successful transmission of *P. tenuis* is a 'game' of compounding odds based on complex interactions of ecological variables. In order for *P. tenuis* to be present within a deer management unit a number of ecological conditions must first be satisfied to facilitate transmission; then these ecological conditions must be optimized in order to maximize transmission.

The higher spring, summer, and fall precipitation associated with the presence of *P. tenuis* is likely due to the influence of precipitation on survival and activity of gastropod hosts and on transmission of first stage larvae to gastropods. Transmission is possibly curtailed when deer feces with *P. tenuis* larvae dries, or when soil conditions are dry because during low moisture conditions gastropods become inactive (Burch 1956). Lankester and Anderson (1968) found that infection of gastropods by first stage larvae of *P. tenuis* was substantially reduced when deer feces were dried or when larvae were placed in dry soil. They speculated that " Larvae deprived of a film of water in which to move may be incapable of invading an intermediate host". Therefore, moist soil conditions, that ultimately depend on precipitation, are necessary to facilitate transmission to gastropods. Rainfall is also important in determining distribution and abundance of terrestrial gastropods (Bruijns et al. 1959). The collection of gastropods during this study revealed a correlation between the abundance of suitable intermediate hosts and presence of *P. tenuis*. The Red River valley in eastern ND, and the southeast corner of MB had both the highest number of suitable gastropod species present, and the highest relative abundance of gastropods. In the grasslands, and agriculturally fragmented landscape of southern SK, not only were there fewer suitable gastropod species collected, but the distribution of these gastropods appeared to be restricted to low-lying swales of willow and aspen, or ephemeral draws and riparian areas.

Climate, particularly moist and warm conditions during spring through summer, likely facilitates transmission of *P. tenuis* by increasing survivorship, and duration of activity of terrestrial gastropods (Bruijns et al. 1959). During dry conditions, or during extreme heat or cold, terrestrial snails move into the litter layer of the soil and/ or aestivate. The likelihood of terrestrial gastropods being infected by *P. tenuis* is dependent on the gastropod encountering viable first stage larvae. Viability of first stage larvae is dependent on suitable conditions of temperature and moisture (Shostak and Samuel 1984). Development of larvae in the terrestrial gastropod is retarded when the gastropod becomes inactive (Lankester and Anderson 1968). Thus, only during conditions of optimal moisture and temperature will gastropods remain active, and larvae development be expedited, thus increasing the odds of a deer ingesting an infective gastropod (*i.e.*, the slug, *Deroceras laeve* becomes inactive at temperatures < 14°C).

The positive correlation of parasite prevalence and winter and fall precipitation is likely due to the positive influence moisture has on the activity and distribution of terrestrial gastropods. Increased precipitation could increase transmission by providing more gastropod habitat and more active gastropods and, therefore, greater chances of gastropods encountering first stage larvae and deer ingesting infective gastropods. The lack of correlation between precipitation and prevalence in MB suggests that precipitation as measured in this study may not be as important as microclimatic moisture conditions in influencing transmission.

I hypothesized that warmer spring, summer, and fall temperatures would be positively correlated with presence and prevalence of *P. tenuis* because warmer temperatures would allow gastropods to be active for longer periods, increasing the likelihood of successful transmission. Likewise, I predicted that DMUs with the hottest summers would be negatively correlated with presence and prevalence, due to high evaporative water loss, resulting in limited distribution and activity of gastropods within these hotter areas.

The lack of any significant positive correlation of temperature with the presence of *P. tenuis* is likely due to how and where temperatures were recorded. In addition, the sample size from some DMUs were not large enough to place high confidence limits on the prevalence reported, thus prevalences stated in some DMUs must be interpreted with caution. Temperature data used in this study were collected 1.5 m above ground, and because of the influence of vegetation, soils, and snow pack on moderating temperature at the soil surface (Stoutjesdijk and Barkman 1992), these temperatures were not likely representative of temperatures experienced by gastropods. A more appropriate method to test the temperature hypothesis would have been to monitor temperature in the litter layer within gastropod and first stage larvae habitat.

The significant negative correlation of presence of *P. tenuis* with colder winter temperatures as revealed by logistic regression analysis could be due to increased survivorship of first stage larvae associated with colder temperatures (Shostak and Samuel 1984). Also, DMUs with the colder monthly temperatures typically have fewer freeze thaw cycles; such cycles have been show to decrease survivorship of first stage larvae (Shostak and Samuel 1984). Alternatively, it is possible that correlation between colder winter temperatures and *P. tenuis* has no ecological significance, but rather may be an artifact of interactions between topography and temperature. The lower elevation DMUs occur throughout the eastern portion of the study area, these eastern-most DMUs are also the units with highest prevalence of *P. tenuis*. These lower elevation areas, influenced by continental winter climates, may simply act as cold pools, which are often colder than adjacent higher elevation areas.

The weak or non significant correlation between winter temperature and presence of *P. tenuis* may reflect the influence of winter snow accumulation. The insulative properties of snow could mitigate sub-zero temperature extremes at the snow/ soil interface making winter ambient temperature an irrelevant influence on survivorship of first stage larvae. Analysis of precipitation in the form of snow revealed no significant correlation between snowfall and presence or absence of *P. tenuis*. I initially hypothesized that areas with greater snowfall and hence a more effective thermal blanket would be more likely to have *P. tenuis* present. The redistribution of fallen snow associated with slope, aspect, wind scouring, and drifting is likely more important than total snowfall in modifying microclimate and determining successful wintering areas for gastropods and larvae.

The odds of encounter between an infected gastropod and a WTD depend on density and spatial overlap of each organism within the environment. Gastropod intermediate hosts must have spatial and temporal overlap with infected deer feces, or at least first stage larvae, which may be dispersed in the soil. Once the gastropod intermediate host is infected with first stage *P. tenuis* larvae, development to third stage larvae is dependent on ambient temperature. Infected gastropods, which occur at very low densities in the field must then be ingested by a WTD; during further development the parasite must then survive an immune response by the WTD, locate a mate within the central nervous system, and pass fertile eggs into the venous blood. A high density of WTD and a high density of infected gastropods, with an associated spatial overlap between the two, will result in optimal transmission conditions. Combinations of, different densities of infected gastropods, different densities of WTD, and degree of spatial overlap likely has a significant effect on transmission of *P tenuis*. Univariate regression analysis revealed a significant positive correlation between the presence of *P. tenuis* and high WTD density. The low predictive power between presence of *P. tenuis* and deer density could be due to several factors, precision of the deer density data is likely very low, also in management units with high deer density, there may be low overlap between deer and infective gastropods.

The relationship between presence of *P. tenuis* and percent forest cover is not surprising given the habitat preference of WTD. The association of *P. tenuis* with forest cover is likely not independent of the presence of WTD. That is, *P. tenuis* is most likely to be found where you have WTD, and WTD are most likely to be found in habitat with a mixture of abundant forage adjacent to forest cover that provides thermal cover and concealment, typically these are landscapes with greater than 50% and less than 75% forested area. In addition to the influence that forest cover may have on WTD habitat, forest cover also likely plays a significant role in moderating microclimate near the forest floor; and hence terrestrial gastropod habitat. Climate has an influence on vegetation, and vegetation in turn plays a significant role in moderating microclimate. Attributes associated with forested areas such as litter layer, organic mat, shrub understorey, and dense tree canopy all have a moderating effect on daily and seasonal fluctuations of temperature and soil moisture (Stoutjesdijk and Barkman 1992).

It was hypothesized that annual climate particularly high precipitation and optimal temperatures would have a measurable effect on annual prevalence. If *P. tenuis* transmission was sensitive to annual climate change, then a significant change in annual climate would result in a predictable year to year change in prevalence of *P. tenuis* (Peterson and Lankester 1991). To detect and significantly test this association of change in climate with change in prevalence would require high sample size and detailed measurement of microclimatic conditions and ecological variables. The influence of sample size and the confidence with which we can determine prevalence within a deer herd as well as a number of other ecological factors may confound any measurable significant correlation of annual climate with annual prevalence. Use of age classes of deer other than fawns in determination of annual changes of prevalence can confound re[illegible] because, if an adult WTD is infected with *P. tenuis*, there is no way of knowing when that adult deer became infected. It may have been infected that season or as a fawn 8-12 years prior (max. life span of free-ranging WTD) and not been re-exposed to infective third stage larvae since the time of initial exposure. The longevity of adult *P. tenuis* is uncertain but is suspected to be relatively long. The life span of *P. odocoilei*, a close relative of *P. tenuis*, has been documented in an experimental infection of a single mule deer (*Odocoileus hemionus*) (Samuel, Unpublished). After initial exposure as a three month old fawn, the mule deer continued to pass larvae until euthanized 9.4 years later. Another close relative of *P. tenuis*, *Elaphostrongylus cervi*, has a reported life span of at least 6 years (Watson 1984). Halvorsen and Andersen (1982) estimated the life span of *Elaphostrongylus rangiferi* at up to 3 years. The suspected long life span of *P. tenuis* further complicates interpretation of prevalence data when trying to determine annual transmission conditions when adult deer are included in the prevalence calculation. In addition to the potential long life span of *P. tenuis*, our limited knowledge on the ability of WTD to mount a successful immune response against, and eliminate infections of, *P. tenuis* further complicates determination of annual transmission conditions. If adult deer are used in the analysis of annual transmission conditions, the question must be asked; are uninfected adults uninfected because: 1) they never ingested third stage *P. tenuis* larvae, or 2) they were infected in the past and were able to eliminate the infection, or 3) they were exposed to third stage *P. tenuis* larvae, and because of previous nematode exposure were able to mount a successful immune response and prevent *P. tenuis* from becoming established.

Some interesting questions regarding the ecology and transmission of *P. tenuis* remain unanswered. Are all WTD infected with *P. tenuis* passing first stage larvae. With *P. tenuis* being dioecious, and the high frequency of single worms recovered from individual deer, some infections may never become patent due to the absence of either sex of worms. A more rigorous test of the ecological conditions that influence transmission of *P. tenuis* would be to monitor prevalence within the fawn cohort each year in conjunction with detailed climate conditions within terrestrial gastropod habitat. This more detailed test of the influence of ecological conditions on transmission would be most easily accomplished at a smaller geographic scale. Mapping gastropod distribution and deer feeding areas would provide an estimate of spatial overlap and thus a measure of transmission potential. Smaller geographic scale would allow more intensive sampling that would in turn facilitate higher confidence in reported prevalences. Necropsy of heads and recovery of adult *P. tenuis* is an extremely labor intensive process, development of a diagnostic method such as a serological test would allow more rapid detection of *P. tenuis* infections.

MANAGEMENT IMPLICATIONS

With the advent of game ranching and the associated movement of WTD from eastern North America to western North America, the potential for accidental introduction of *P. tenuis* into susceptible populations of ungulates is a real one. The high number of ungulates being bought, sold and transported throughout North America confirms this potential threat.

A review of the predicament Alberta game ranchers recently faced brought the issue of accidental introduction of an ungulate pathogen associated with game ranched animals to the forefront. In 1992, detection of bovine tuberculosis in privately owned elk in Alberta, and subsequent retracing of the movement of potentially infected animals, resulted in a depopulation program to control the further spread of tuberculosis. The campaign to eradicate bovine tuberculosis concluded with the depopulation of 2 500 captive elk and other susceptible animals on 13 of approximately 120 game farms in Alberta (M.J. Pybus pers. comm.). Fortunately the detection of tuberculosis is relatively easy using serological tests; so too is control, because tuberculosis organisms cannot persist in the environment outside its living host. In comparison, *P. tenuis* is difficult to detect in the living definitive host because of its complex life cycle. Once established in a free ranging deer population, *P. tenuis*, would be virtually impossible to eliminate.

The presence of *P. tenuis* in western ND and eastern SK is of particular interest to game ranchers. The confirmed presence of this parasite in SK casts political doubt on the need for restricting importation of ungulates into SK from areas to the east because the parasite of concern has been reported there. While some individuals in SK will take that side, game managers will likely still want to be very conservative regarding inter-provincial movements of animals to ensure that this pathogenic parasite is not introduced to susceptible ungulate herds.

In Alberta, where there was concern that *P. tenuis* could be accidentally introduced due to the translocation of game ranched elk and WTD, importation of such animals was prohibited in 1988. This concern that game ranched elk and WTD may serve as a vector for introduction of *P. tenuis* was heightened when Samuel et al. (1992) found that some elk survived infections of *P. tenuis* and shed viable larvae of *P. tenuis*. There is little doubt that game ranching could facilitate introduction of *P. tenuis* to non-endemic areas including western Canada.

The important question for many jurisdictions remains whether or not *P. tenuis* could become locally established, if introduced. In Alberta, terrestrial gastropods known to be intermediate hosts for *P. tenuis* are present in central (VanEs and Boag 1981) and western parts of the province (Samuel et al. 1984). Three of the four most abundant and widely distributed terrestrial mollusks in southern Alberta, *Discus cronkhitei, Zonitoides arboreus,* and *Deroceras laeve* (pers. comm. P.D. Lewis, University of Lethbridge), are known intermediate hosts of *P. tenuis.* The presence and abundance of these terrestrial gastropods in portions of Alberta, indicate that climate is suitable for known intermediate hosts. Whether or not the Alberta climate is suitable for survival of viable first stage larvae, or is warm enough for long enough to permit development of larvae to the infective stage in gastropods remains a question.

White-tailed deer densities in Alberta (Wishart pers. comm.) are typically lower than WTD populations in the east; however, threshold densities of deer required to permit establishment of *P. tenuis* have yet to be determined.

To date we have no knowledge of how gastropod density and distribution in Alberta compares to areas where *P. tenuis* is common. Suitability of climate for *P. tenuis* presence in Edmonton, Alberta (53° 34' N, 113° 31' W) was evaluated using the univariate regression models generated by the ND and MB data. Spring, and fall precipitation in Edmonton predicts a 20% and 15% probability respectively, that *P. tenuis* was present. The summer precipitation model predicted an 88% probability that *P. tenuis* was present (Figure 30). The summer and fall temperature model was not significant therefore temperature conditions for Edmonton could not be evaluated (Figure 31).

Parelaphostrongylus odocoilei, a species closely related to *P. tenuis,* is present in mule deer of western Alberta. Its presence suggests that ecological conditions; *i.e.,* precipitation, temperature, and suitable gastropods that facilitate transmission of *P. odocoilei* could also facilitate successful establishment of *P. tenuis* if it were introduced. The only evidence to cast doubt on drawing this parallel between the *Parelaphostrongylus* spp. is that first stage larvae of *P. odocoilei* may be better adapted to northern climates by being more freeze tolerant than *P. tenuis* larvae (Shostak and Samuel 1984). Once introduced, establishment of *P. tenuis* could occur rapidly given the high number of first stage larvae in feces of infected deer (Samuel unpubl.) and relatively high defecation rate (12 pellet groups/ day) of WTD (Rogers

1987). It would not take a high density of WTD to contaminate a relatively large area in a short period of time.

The positive correlation of presence of *P. tenuis* within areas of higher precipitation suggests that the lower rainfalls associated with the prairie biome may indeed act as a natural ecological barrier for westward movement of *P. tenuis*. If one of our management objectives is to prevent establishment of *P. tenuis* in the west then game managers, in addition to all ecological variables, must also consider the effects of current landuse. Current landuse practices such as irrigation, and elimination of natural ecosystem processes (*i.e.*, seasonal grassland fires), could eliminate this natural arid barrier. Irrigation farming, if extensive enough, could provide a 'high precipitation bridge' across the grasslands. Historic wildfires that swept across the prairie biome each spring prevented encroachment of trees and shrubs that now provide cover for both gastropods and WTD. Human-induced fragmentation of the boreal mixedwood forest biome associated with agricultural expansion increased the habitat and northern range of WTD. Elimination of many natural predators of WTD and winter feeding programs maintain un-naturally high WTD densities. It is possible that the extensive cultivation of historic natural grasslands and reduction in gastropod diversity and abundance associated with cultivation may accentuate the climatic barrier of the grassland biome or at least compensate for the elimination of fire; however, other factors such as irrigation, high deer density, and forest cover may erode what was once a natural barrier. Game managers must start addressing management issues in broader time periods and larger landscape scales to ensure that wildlife objectives do not disrupt ecological processes and that we do not facilitate development of undesirable conditions such as presence of *P. tenuis* in the West.

The question of whether or not *P. tenuis* can become established west of 100° longitude remains unanswered. The risk of accidental introduction is apparent and the consequences for susceptible native ungulates dire. Game managers must take conservative measures to ensure that we do not 'find out the hard way' if this parasite could become established in Alberta. If the present demand to import what could be potentially infected ungulates continues, existing legislation restricting such imports should remain in place. Development of an effective diagnostic procedure could allow relaxation of the importation ban only if the procedure will never err with a false negative result. Refinement of the multiple regression model through intensive research could provide game managers with a tool to evaluate the probability that *P. tenuis* could become established in an area given local ecological conditions *i.e.*, precipitation, temperature, % land forested, deer density, gastropod hosts.

Table 1. Some reports of natural and experimental occurrence of *Parelaphostrongylus tenuis* in ungulates.

Order	Family	Species	Nat./ Exp.	Reference
Artiodactyla	Camelidae	*Lama glama*	Nat.	Baumgartner et al. 1985, Krogdahl et al. 1987, O'Brien et al. 1986 Lunn and Hinchcliff 1989
			Exp.	Foreyt et al. 1991
		Lama guanacoe	Nat.	Brown et al. 1978
	Cervidae	*Alces alces*	Exp.	Anderson 1964
			Nat.	Smithe et al. 1964, Anderson 1965a, Kurtz et al. 1966, Karns 1967, Smith and Archibald 1967, Behrend and Witter 1968
		Cervus elaphus	Exp.	Anderson et al. 1966, Samuel et al. 1992
			Nat.	Carpenter et al. 1973
		Odocoileus virginianus	See Table 2.	
		Odocoileus hemionus hemionus	Exp.	Anderson et al. 1966
		Rangifer tarandus	Exp.	Anderson and Strelive 1968
		Dama dama	Exp.	Kister et al. 1977, Pybus et al. 1992
	Bovidae	*Capra hircus*	Nat.	Mayhew et al. 1976, Guthery et a. 1979, Dew et al. 1992, Kopcha et al. 1989
		Oryx dammah	Nat.	Nichols et al. 1986
		Ovis aries	Exp.	Anderson and Strelive 1966b, Jortner et al. 1985
			Nat.	Kennedy et al. 1952, Whitlock 1952, 1959; Nielson and Aftosmis 1964, Alden et al. 1975, O'Brien et al. 1986
		Ovis canadensis	Exp	Samuel pers. comm.
		Tragelaphus eurycerus	Nat.	Nichols et al. 1986

Table 2. Prevalence of *Parelaphostrongylus tenuis* in white-tailed deer in North America.

State/ Province	% Infected	Reference
Alberta	0	Samuel and Holmes 1974
Alabama	34.5	Comer et al. 1991
Arkansas	52.6	Comer et al. 1991
Florida	0.3	Comer et al. 1991
Georgia	44.9	Comer et al. 1991
Idaho	0	Foreyt and Compton 1991
Indiana	33	Platt 1989
Iowa	45	Jarvinen and Hedberg 1993
Kentucky	72.7	Comer et al. 1991
Louisiana	36.0	Comer et al. 1991
Maine	84, 72, 85	Behrend and Witter 1968, Gilbert 1973, Bogaczyk 1990, respectively
Manitoba	10	Bindernagel and Anderson 1972
Maryland	61.1	Comer et al. 1991
Michigan	46, 57	Degiusti 1955 and Degiusti 1963, respectively
Minnesota	33, 49, 44	Loken et al. 1965, Karns 1967, Peterson & Lankester 1991, respectively
Mississippi	42.2	Comer et al. 1991
New Brunswick	60	Upshall et al. 1987
New Hampshire	62	Thurston and Strout 1978
New Jersey	40	Pursglove 1977
New York	72, 46	Behrend 1970 and Garner and Porter 1991, respectively
North Carolina	70, 58.4	Prestwood and Smith 1969 and Comer et al. 1991, respectively
Nova Scotia	51	Thomas and Dodds 1988
Oklahoma	52, 90, 39	Carpenter et al. 1972, Pursglove 1977, Kocan et al. 1982
Ontario	33, 41, 61	Anderson 1956, Anderson 1963a, Lankester and Anderson 1968
Pennsylvania	75,81,	Alibasoglu et al. 1961, Samuel and Beaudoin 1966
Pennsylvania	(30, 76), (42, 68, 72)	Beaudoin et al. 1970, Woolf et al. 1977
Quebec	30	Bindernagel and Anderson 1972
Saskatchewan	0	Bindernagel and Anderson 1972
South Carolina	1.0	Comer et al. 1991
Tennessee	57.5	Comer et al. 1991
Texas	0	Samuel 1969
Virginia	73, 27.9	Dudak et al. 1965, Comer et al. 1991
West Virginia	73, 59.1	Dudak et al. 1965, Comer et al. 1991
Wisconsin	38, 78	Samuel and Trainer 1969, Dew 1988

Table 3. Intensity of *Parelaphostrongylus tenuis* infections reported in free ranging white-tailed deer of eastern North America.

Mean Intensity	Location	Reference
7.3	Arkansas	Owen 1974
3.8	Georgia	Prestwood and Smith 1969
3.6 (maximum 16)	Iowa	Jarvinen and Hedberg 1993
3.3	Maryland	Prestwood and Smith 1969
2.2 fawns, 3.9 adults	Maine	Gilbert 1973
2.5 fawns, 3.9 yearlings + adults	Maine	Bogaczyk 1993
2.1 (maximum 9)	Minnesota	Karns 1967
4.5	New Brunswick & Nova Scotia	Smith et al. 1965
2.3 (maximum 9)	New Hampshire	Thurston and Strout 1978
1.5 -8.7	New York	Behrend 1970
5.2 -6.5	North Carolina	Prestwood and Smith 1969
3.9 (maximum 20)	Ontario	Anderson 1963
4.2	Virginia	Prestwood and Smith 1969
1.5 - 5.3	West Virginia	Prestwood and Smith 1969
10 (single deer)	Wisconsin	Eckroade et al. 1970

Table 4. Prevalence of *Parelaphostrongylus tenuis* in white-tailed deer for all white-tailed deer sampled in Manitoba, North Dakota, and Saskatchewan.

	Percent Deer Infected	Number Deer Infected	Number Deer Examined
Manitoba	18.6	149	799
North Dakota	8.4	45	538
Saskatchewan	0.2	1	565
TOTAL	10.3	195	1902

Table 5. Prevalence of *Parelaphostrongylus tenuis* in white-tailed deer by sex for all white-tailed deer sampled in Manitoba, North Dakota, and Saskatchewan.

	Sex			
	Male		Female	
Manitoba	92/ 486	(18.9)*	56/ 311	(18.0)
North Dakota	12/ 212	(5.7)	33/ 326	(10.1)
Saskatchewan	0/ 286	(0)	1/ 279	(0.36)
TOTAL	104/ 984	(10.6)	90/ 916	(9.83)

*number of white-tailed deer infected /number of white-tailed deer examined (% of white-tailed deer infected)
◊sex could not be determined for two deer, therefore n = 1900.

Table 6. Prevalence of *Parelaphostrongylus tenuis* infections in white-tailed deer from Manitoba, North Dakota, and Saskatchewan.

	Fawns		Yearlings		Adults	
	Males	Females	Males	Females	Males	Females
Manitoba	9/ 86 (10.5)*	6/ 74 (8.1)	39/ 193 (20.2)	9/ 61 (14.8)	43/ 202 (21.3)	41/ 176 (23.3)
North Dakota	4/ 83 (4.8)	1/ 46 (2.2)	5/ 103 (4.9)	8/ 94 (8.5)	3/ 26 (11.5)	24/ 185 (13.0)
Saskatchewan	0/ 59 (0)	0/ 67 (0)	0/ 103 (0)	0/ 63 (0)	0/ 122 (0)	1/ 148 (0.68)
TOTAL	13/ 228 (5.7)	7/ 187 (3.7)	44/ 399 (11.0)	17/ 218 (7.8)	46/ 350 (13.1)	66/ 509 (13.0

*number of white-tailed deer infected /number of white-tailed deer examined (% of white-tailed deer infected)

Table 7. Prevalence of *Parelaphostrongylus tenuis* in white-tailed deer by age class for all white-tailed deer sampled in Manitoba, North Dakota, and Saskatchewan.

	Age of Deer					
	Fawn		Yearling		Adult	
Manitoba	15/ 160	(9.4)*	48/ 254	(18.9)	84/ 378	(22.2)
North Dakota	5/ 129	(3.9)	13/ 197	(6.6)	27/ 211	(12.8)
Saskatchewan	0/ 126	(0)	0/ 166	(0)	1/ 270	(0.4)
TOTAL	20/ 415	(4.8)	61/ 617	(9.9)	112/ 859	(13.0)

*number of white-tailed deer infected /number of white-tailed deer examined (% of white-tailed deer infected)
◊sex could not be determined for 11 deer, therefore n = 1891.

Table 8. Intensity of infection of *Parelaphostrongylus tenuis* infections in white-tailed deer by age class in Manitoba, North Dakota, and Saskatchewan.

	Mean number of worms		
	Fawns	Yearlings	Adults
Manitoba	1.71 ±0.91†	2.42 ±2.00	2.48 ±1.96
North Dakota	3.50 ±3.70	1.31 ±0.75	2.28 ±1.4
Saskatchewan	0	0	1*

† mean ± Std. Dev.
* single *P. tenuis* recovered from one deer

Table 9. Species of terrestrial gastropods collected within the study area.

Gastropods	ND	SK	MB	
Snails				
Cochlicopa lubrica (Cionella)	**		**	†
Discus cronkhitei	**	**	**	†
Euconulus fulvus	*	*	*	
Gastrocopta armifera	*		*	†
Gastrocopta tappaniana	*		*	
Punctum minutissumum	*	*	*	
Pupilla muscorum		*	*	
Retinella electrina	**		**	†
Strobilops aenea			*	†
Strobilops labyrinthica			*	†
Succinea ovalis	**	**	**	†
Vallonia spp.	*	*	*	
Vertigo spp.	*	*	*	†
Vitrina alaskana	*	*		
Zonitoides arboreus	**	**	**	†
Zoogenets harpa	*		*	
Slugs				
Deroceras laeve	**	**	**	†
Species of known intermediate hosts	6	4	6	
Species of gastropods	14	10	16	

** known intermediate host

† previously examined for third stage larvae

Table 10. Ecological variables that generated a significant univariate logistic regression model predicting the presence or absence of *Parelaphostrongylus tenuis* within a deer management unit.

Ecological Variables	r^2	P Value
Precipitation Mean, March	0.06	< 0.001
Precipitation Mean, April	0.08	0.003
Precipitation Mean, May	0.06	0.01
Precipitation Mean, June	0.05	0.015
Precipitation Mean, July	0.22	< 0.001
Precipitation Mean, August	0.33	< 0.001
Precipitation Mean, September	0.21	< 0.001
Precipitation Mean, October	0.19	< 0.001
Precipitation Mean, November	0.06	0.007
Temperature Mean, December	0.04	0.024
Temperature Mean, January	0.04	0.026
Temperature Mean, February	0.07	0.02
Precipitation Seasonal, Spring	0.13	< 0.001
Precipitation Seasonal, Summer	0.32	< 0.001
Precipitation Seasonal, Fall	0.19	< 0.001
Temperature Seasonal, Winter	0.05	0.014

Table 11. Ecological variables loaded in multiple logistic regression analysis and respective r^2 values ($p < 0.001$).

Ecological Variable	r^2
Summ Precip	0.32
Summ Precip/ Fall Precip	0.34
Summ Precip/ Fall Precip/ Winter Temp	0.34
Summ Precip/ Fall Precip/ Winter Temp/ Spring Temp	0.50
Summ Precip/ Fall Precip/ Winter Temp/ Spring Temp/ %Forested	**0.56**
Summ Precip/ Fall Precip/ Winter Temp/ Spring Temp/ %Forested/ Deer density	0.57
Summ Precip/ Fall Precip/ Winter Temp/ Spring Temp/ %Forested/ Deer density/ Elevation	0.58

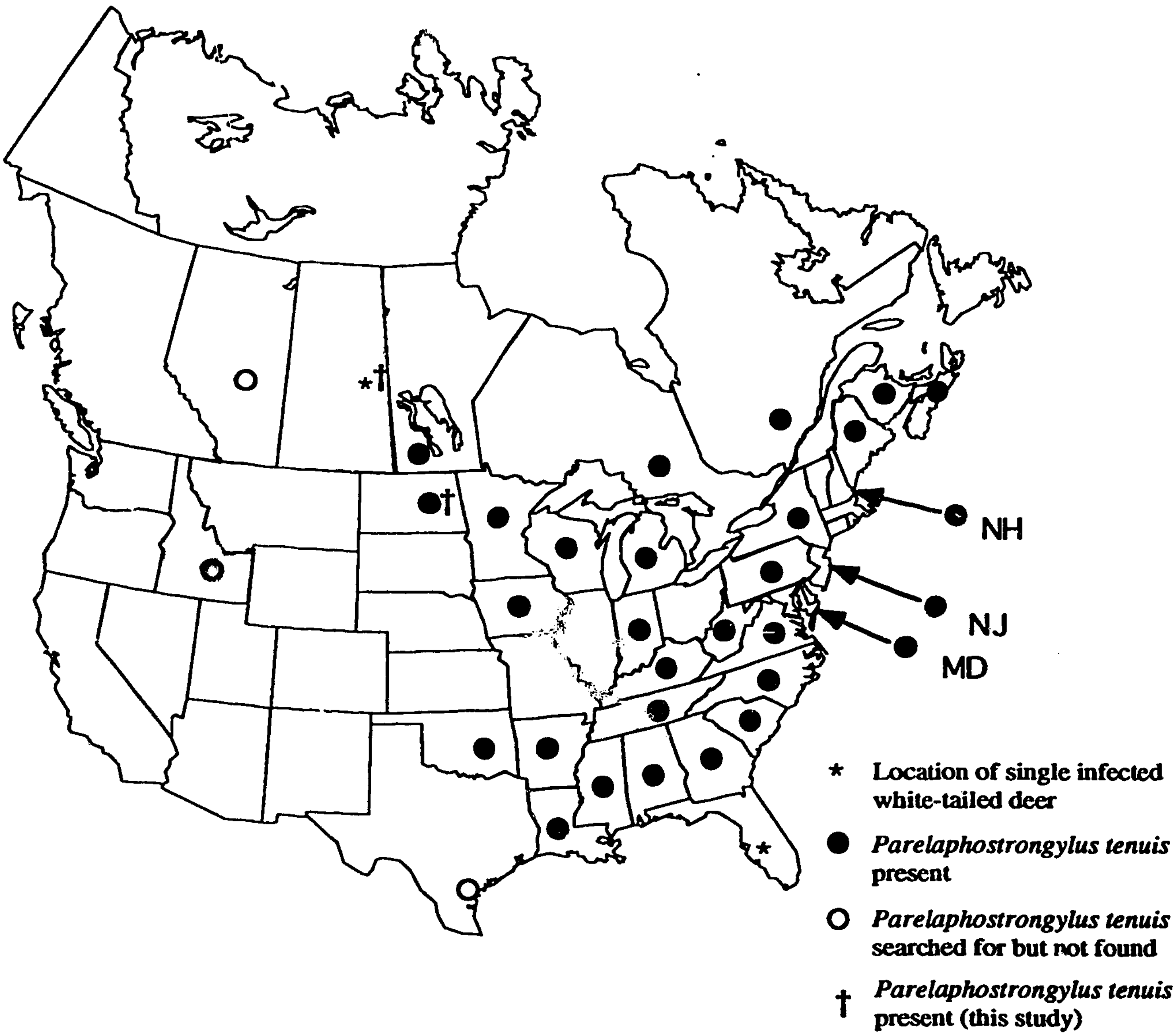
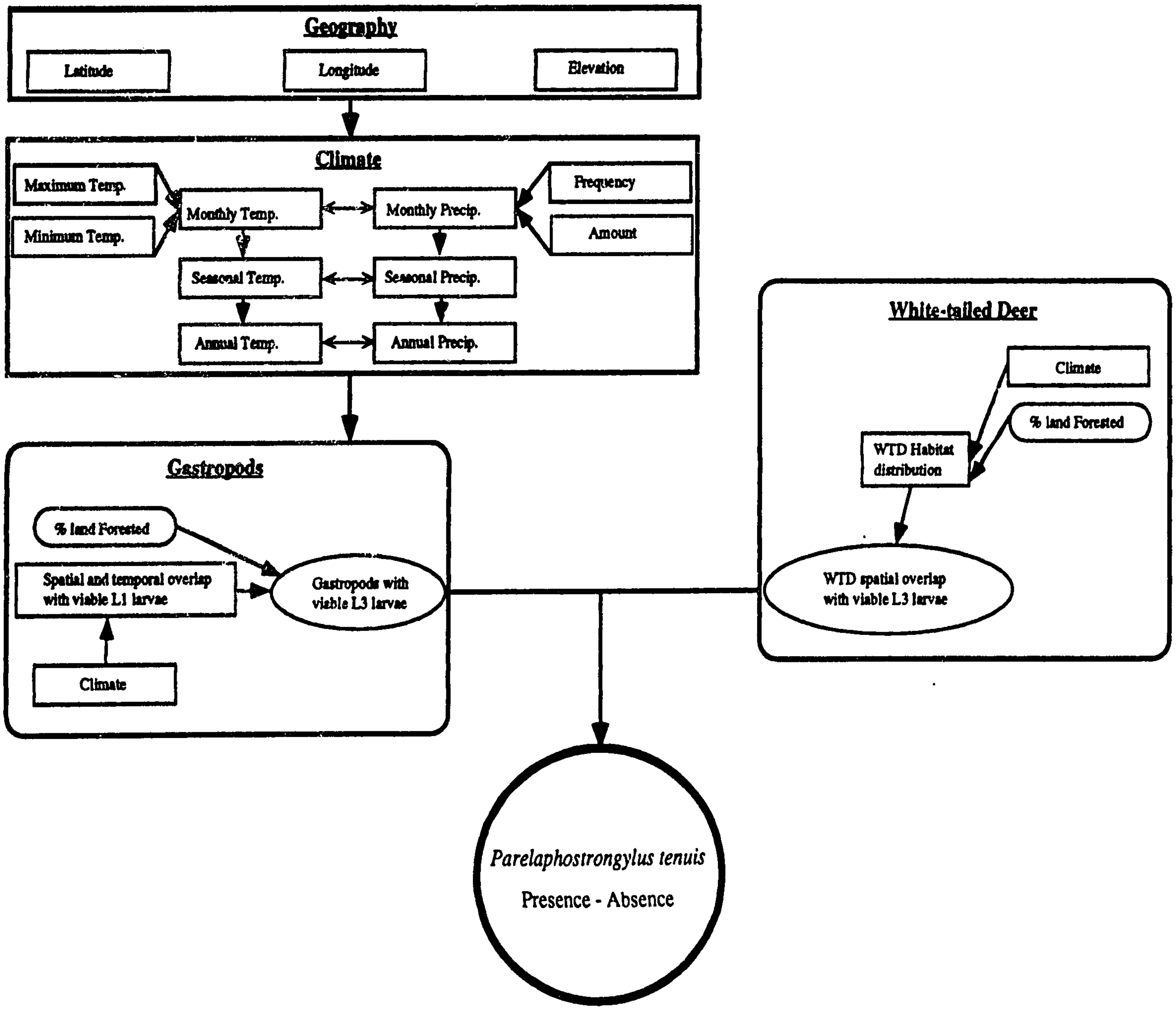


Figure 1. Provinces and states where white-tailed deer have been examined for *Parelaphostrongylus tenuis.*

Figure 2. Path analysis of ecological variables potentially associated with the presence or absence of *Parelaphostrongylus tenuis*.



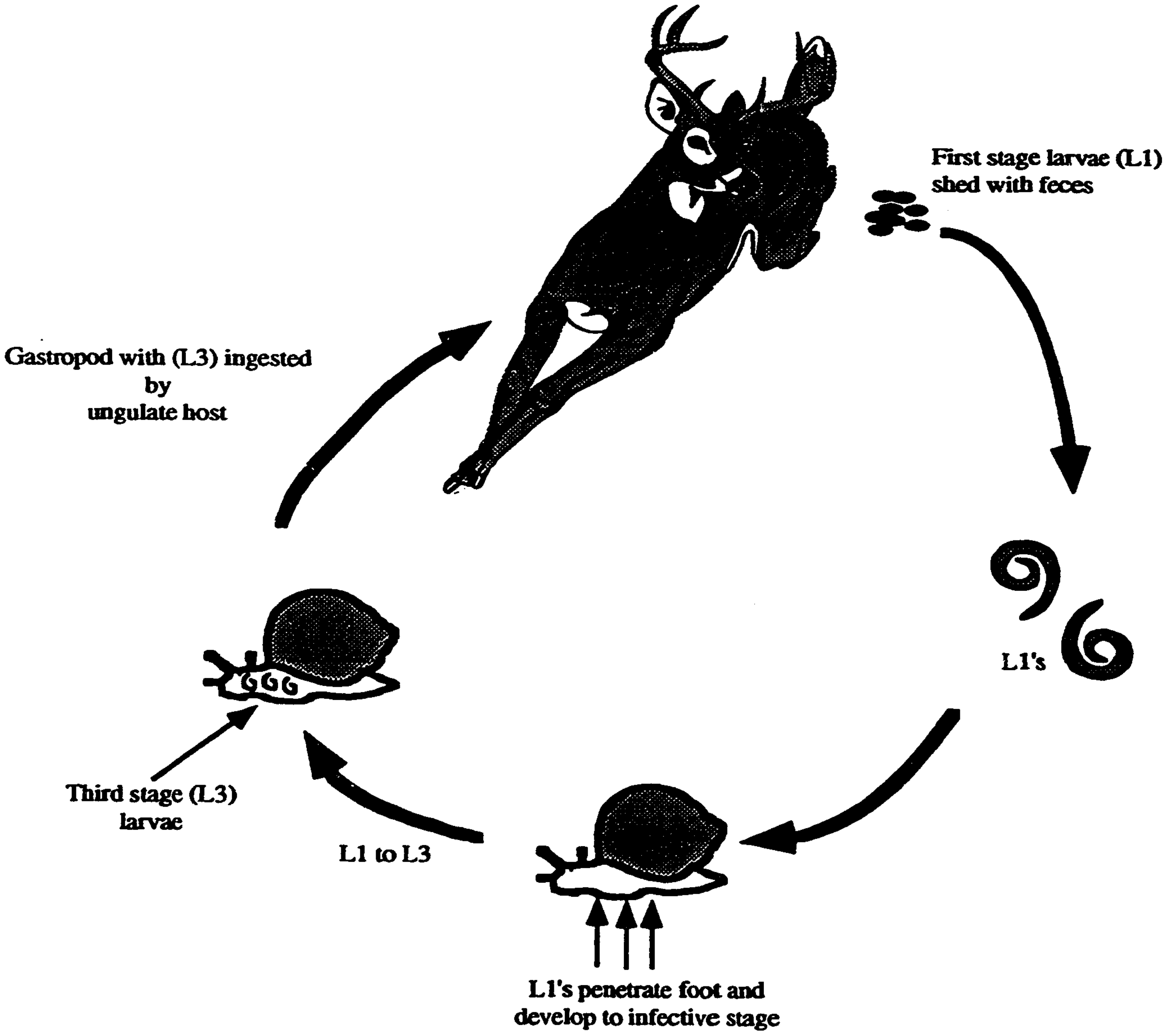


Figure 3. Life cycle of *Parelaphostrongylus tenuis*

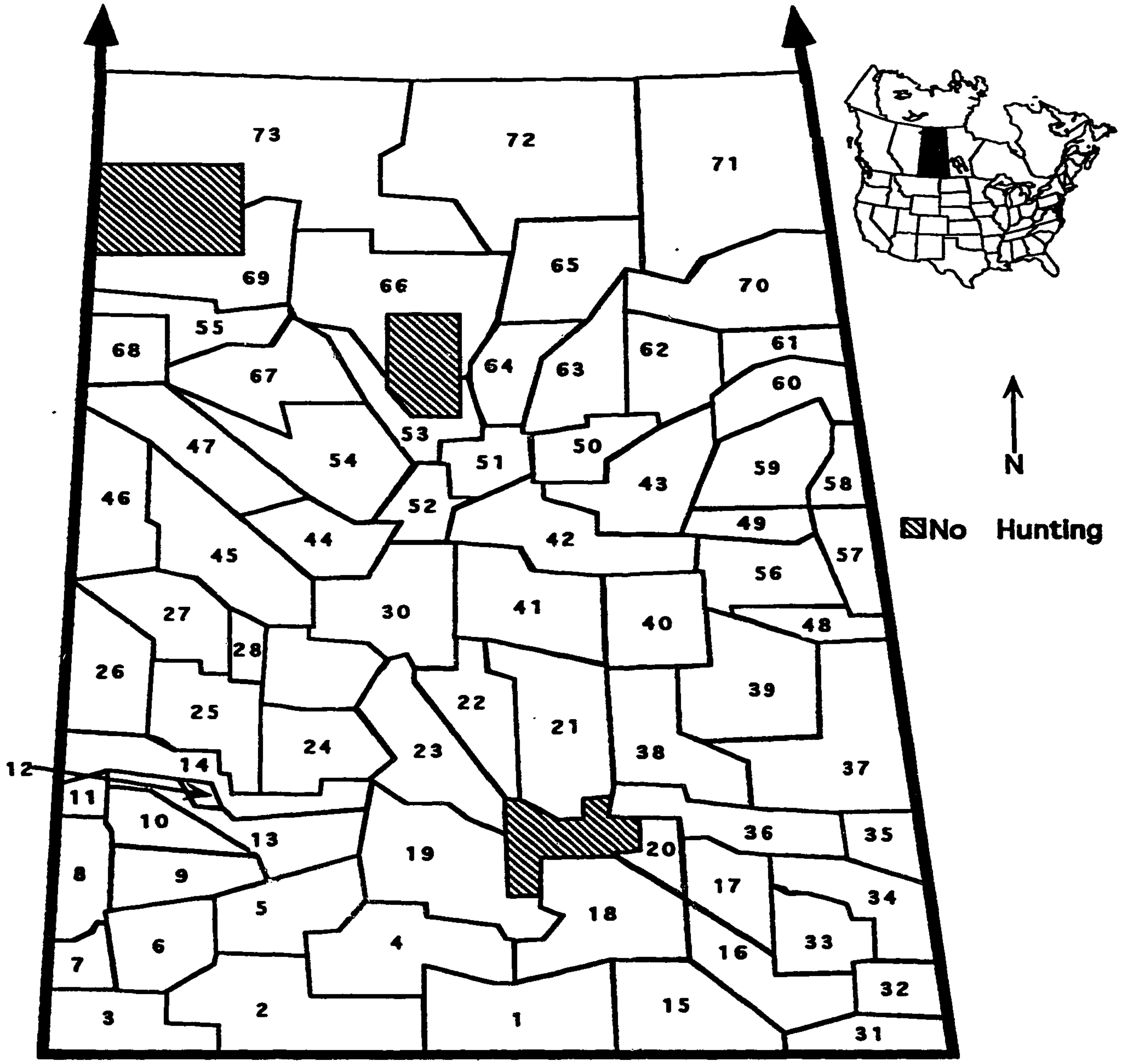


Figure 4. Deer Management Units (Wildlife Management Zones) in Saskatchewan, 1989 and 1990 (northern zones not indicated). Not to scale.

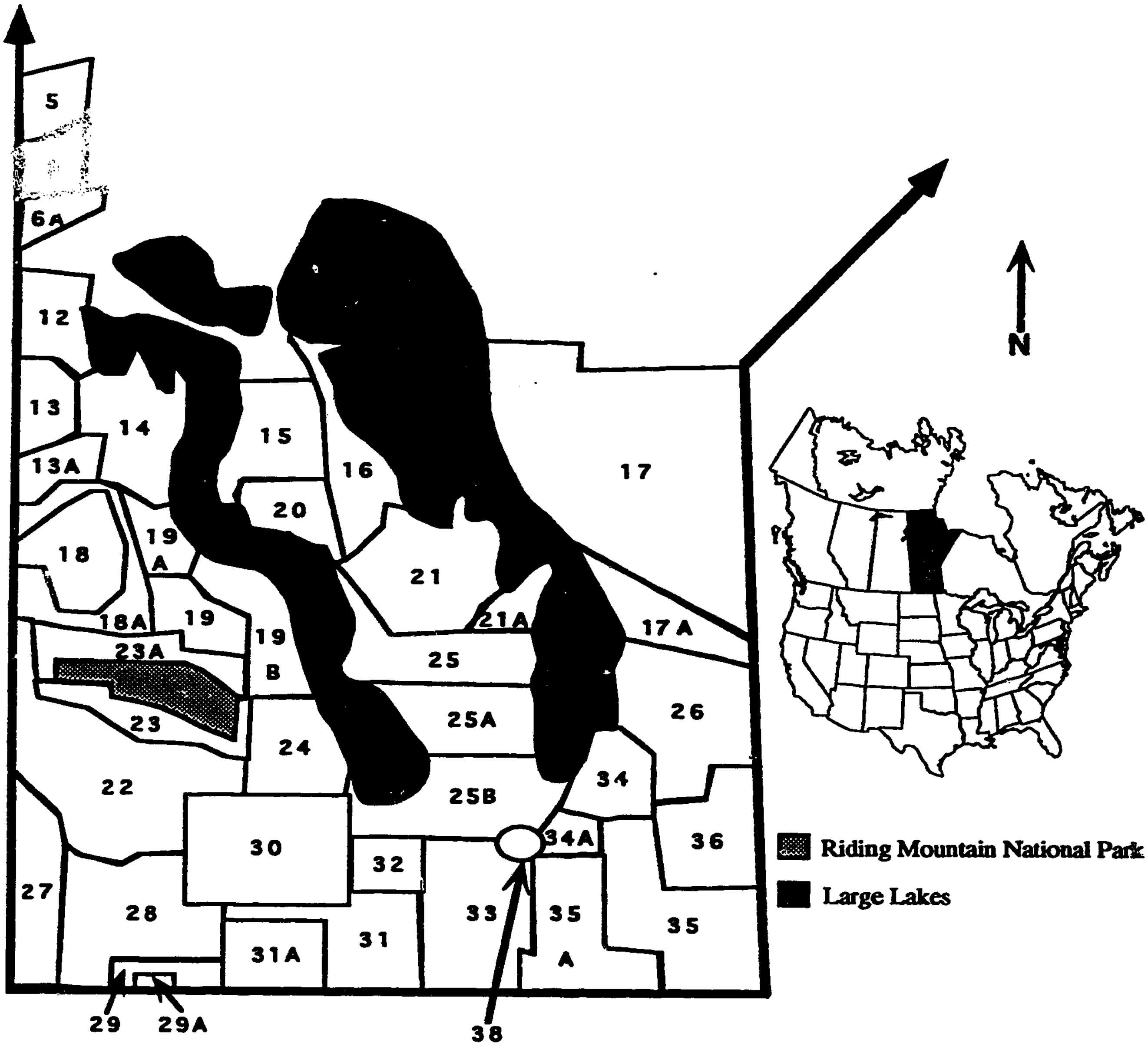


Figure 5. Deer Management Units (Gun Hunting Areas) in Manitoba, 1989 and 1990 (northern units not indicated). Not to scale.

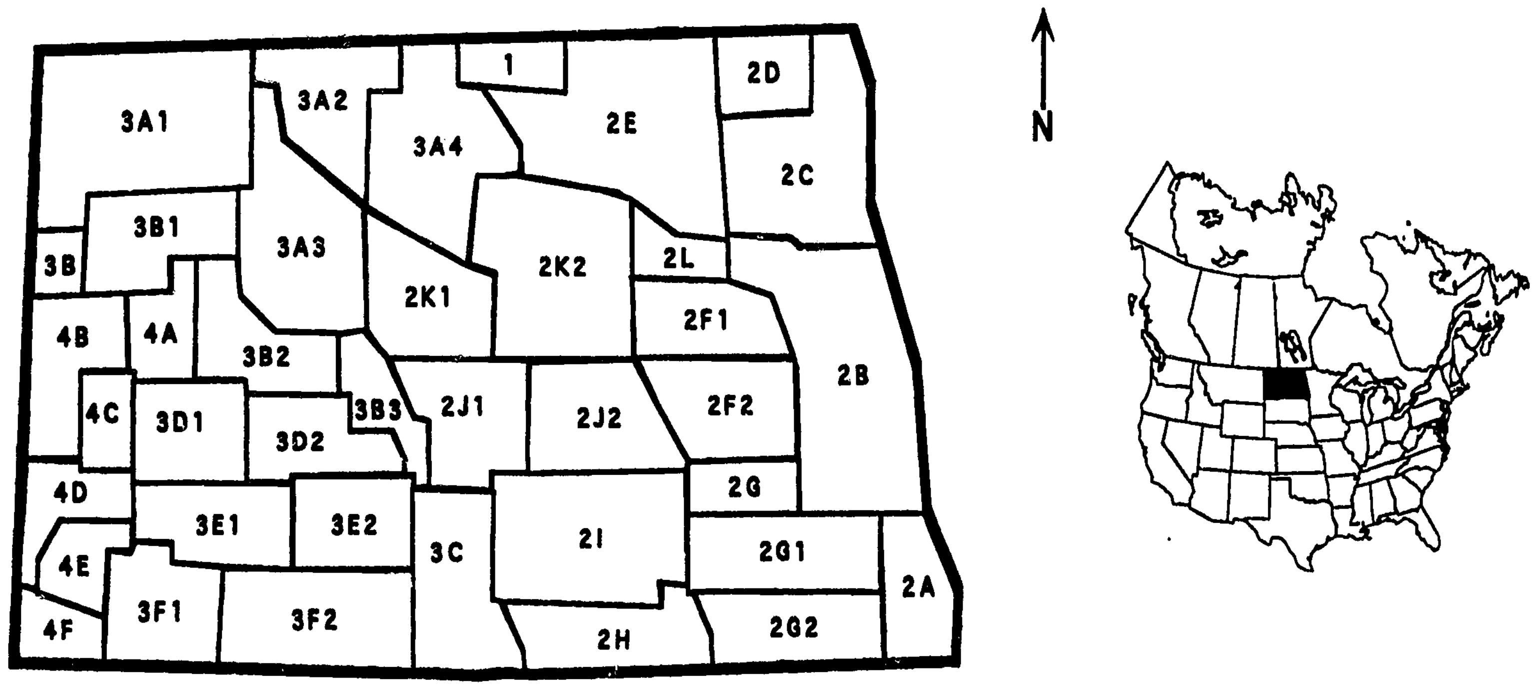


Figure 6. Deer Management Units (Gun Hunting Units) in North Dakota, 1989 and 1990.
Not to scale.

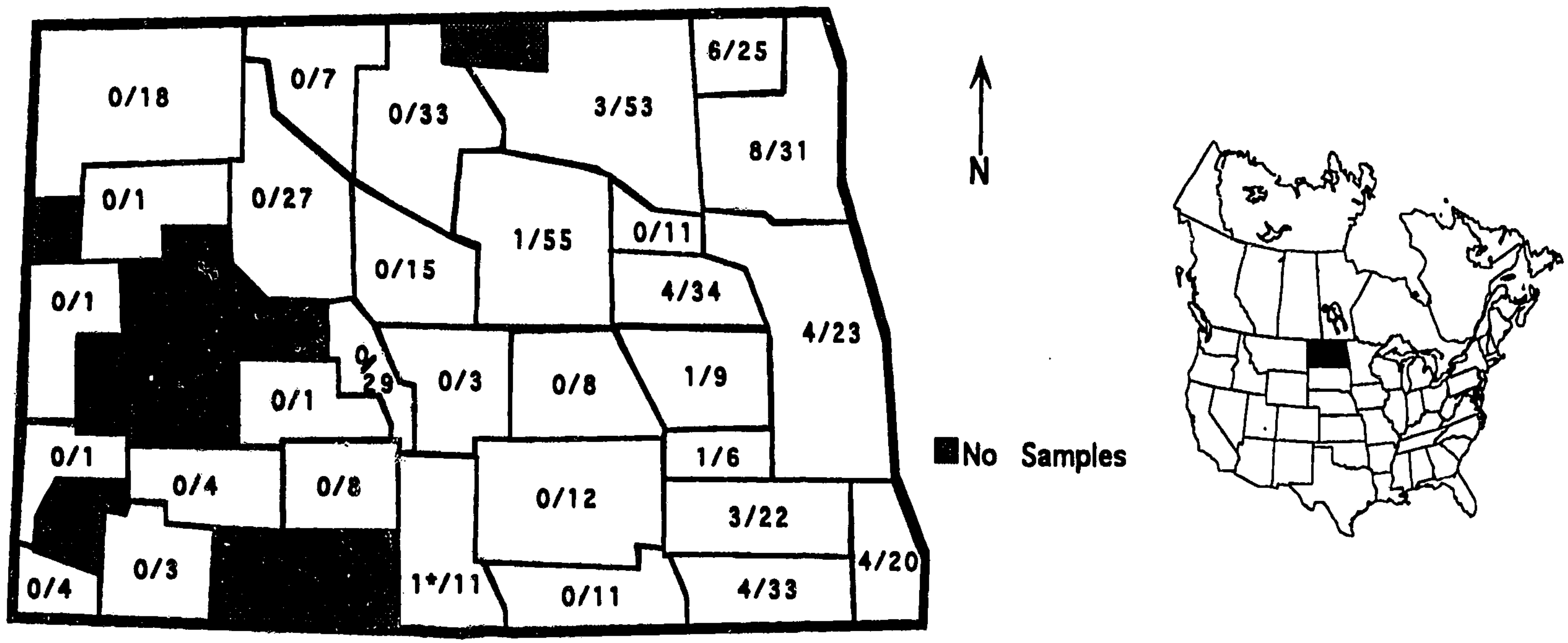


Figure 7. Number of white-tailed deer examined and number infected with *P. tenuis* in North Dakota Gun Hunting Units.
Gun Hunting Unit of origin could not be determined for 18 white-tailed deer heads (4/ 18 infected), thus these heads are not indicated here. *Exact location within management unit unknown.

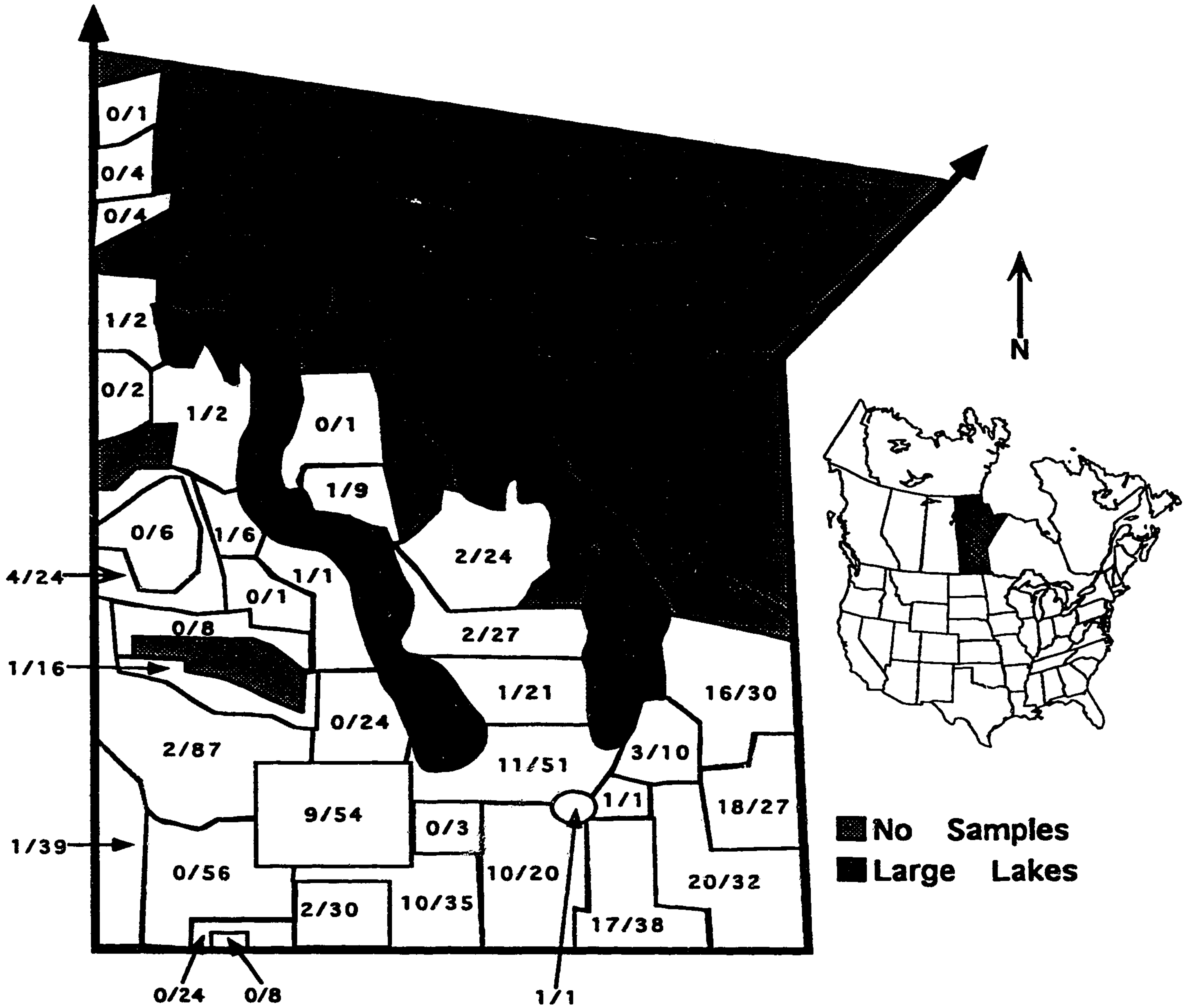


Figure 8. Number of white-tailed deer examined and number infected with *P. tenuis* in Gun Hunting Areas in Manitoba. Gun Hunting Area of origin could not be determined for 70 white-tailed deer heads (13/ 70 infected), thus these heads are not indicated here.

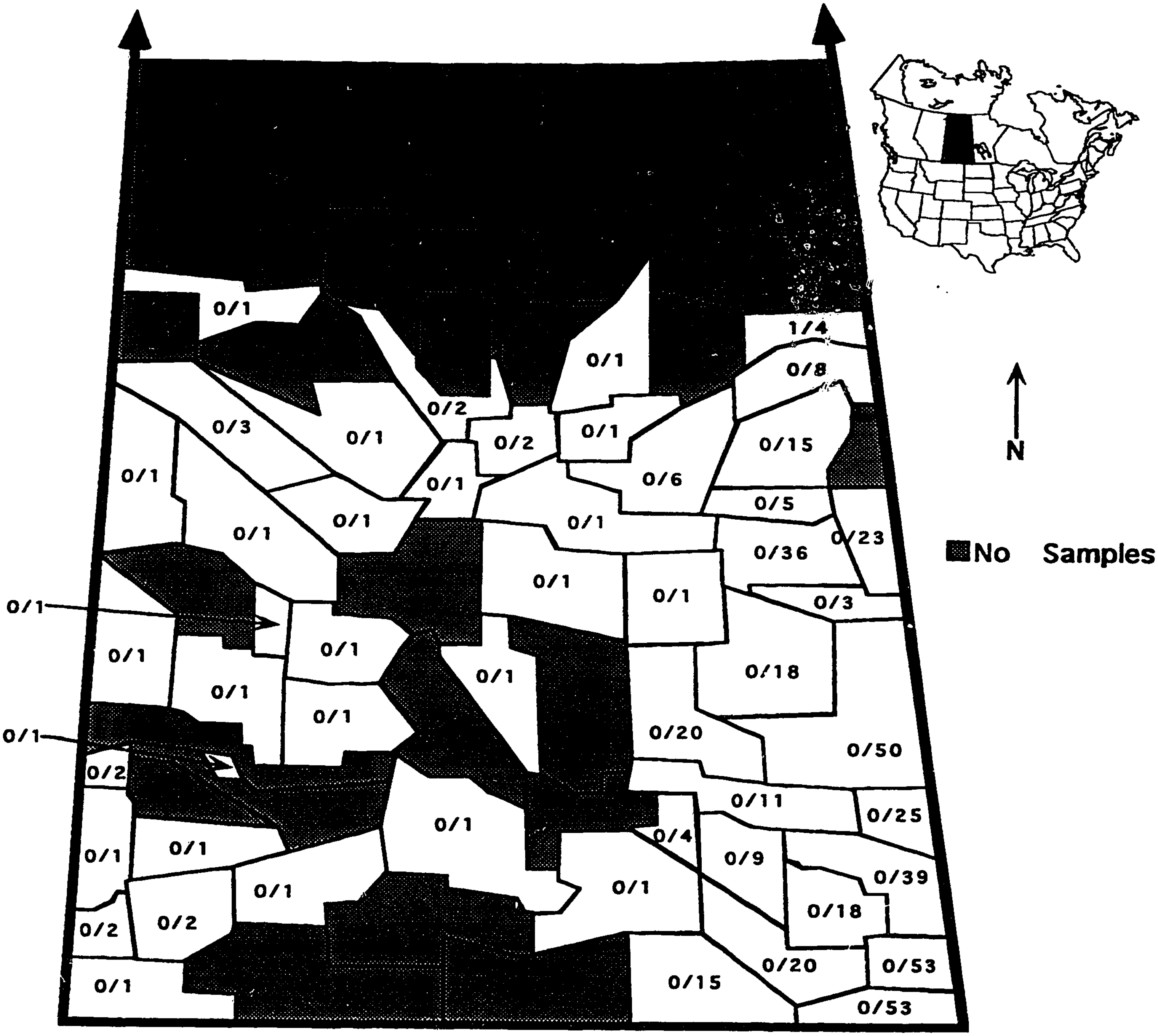


Figure 9. Number of white-tailed deer examined and number infected with *P. tenuis* in Wildlife Management Zones in Saskatchewan. Wildlife Management Zone of origin could not be determined for 93 white-tailed deer heads, thus these heads are not indicated here.

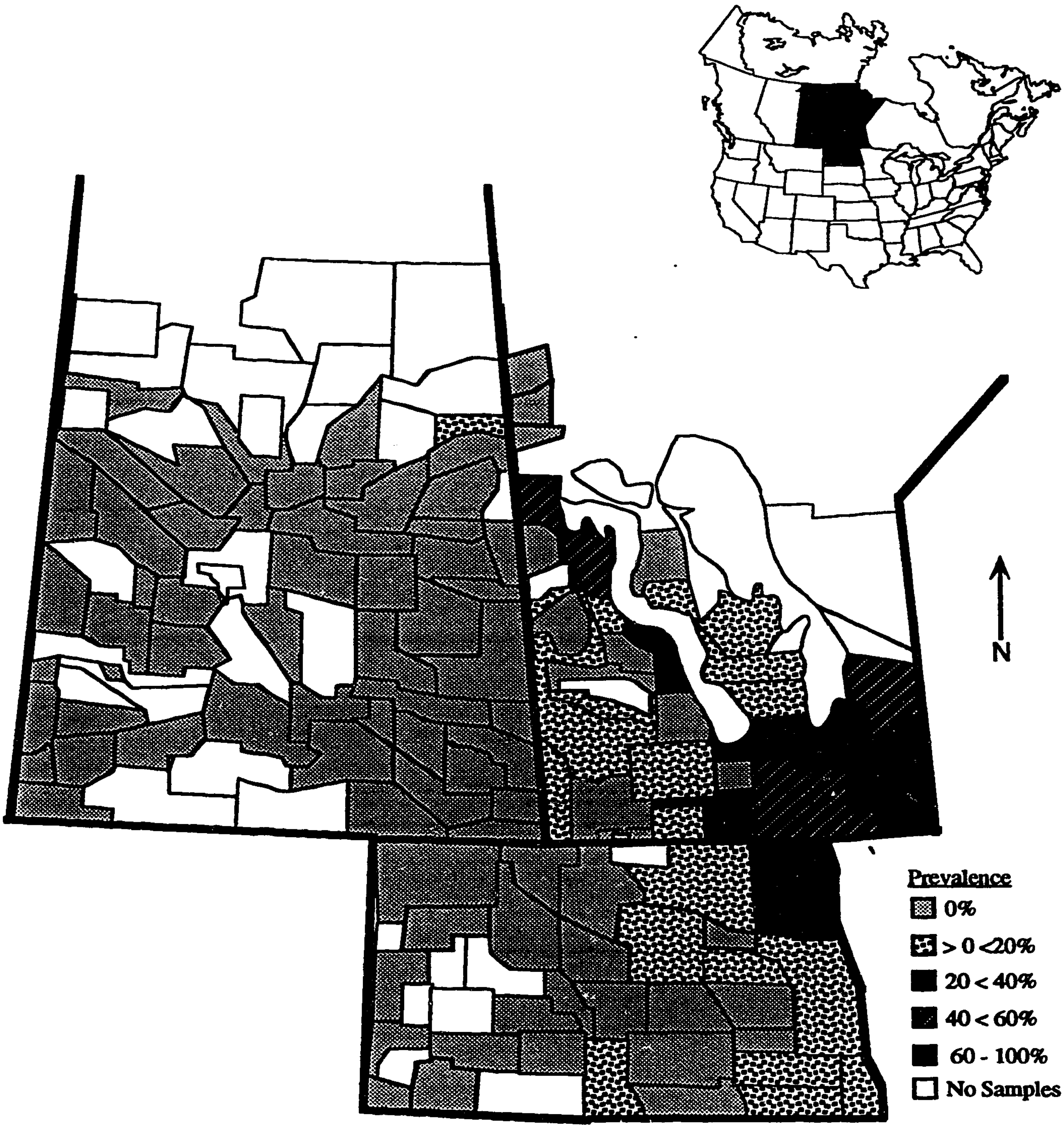


Figure 10. Deer Management Units in Saskatchewan, Manitoba, and North Dakota with white-tailed deer examined for *P. tenuis* and reported prevalence of *P. tenuis* for all white-tailed deer necropsied. A total of 1901 deer heads were included in analysis. All white-tailed deer were killed in 1987 (2)*, 1988 (28), 1989 (919), 1990 (946), 1991 (1), and year unknown (5). Not to scale.
* Denotes sample size.

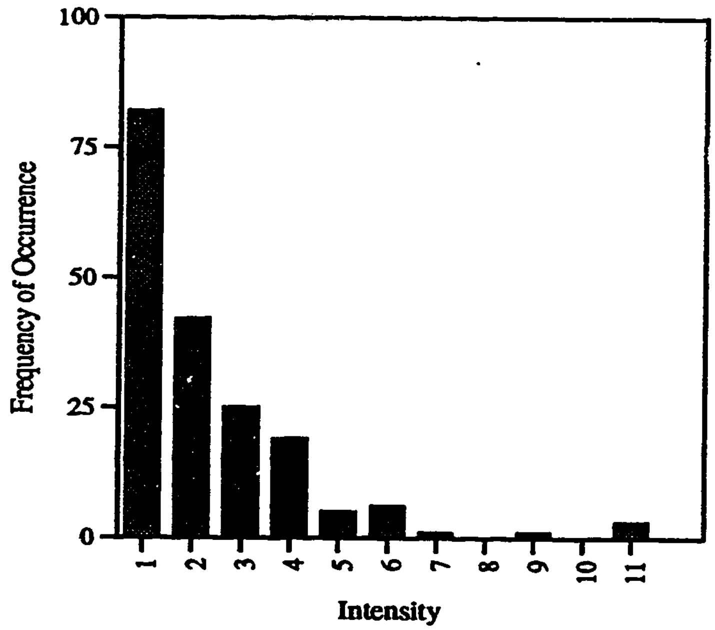


Figure 11. Frequency distribution of intensity (number of parasites/ infected host) of *Parelaphostrongylus tenuis* for infected white-tailed deer (n = 187).

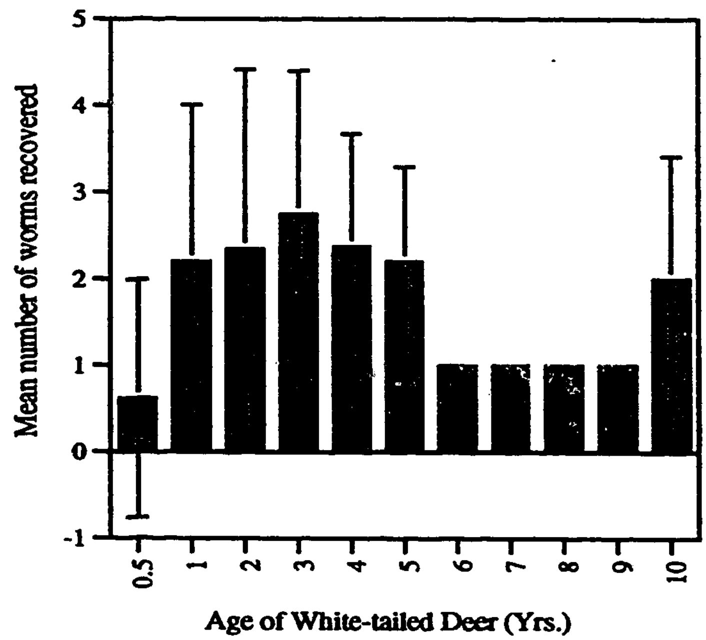


Figure 12. Mean number of *Parelaphostrongylus tenuis* (and standard error) in each infected deer (n = 155) of known age.

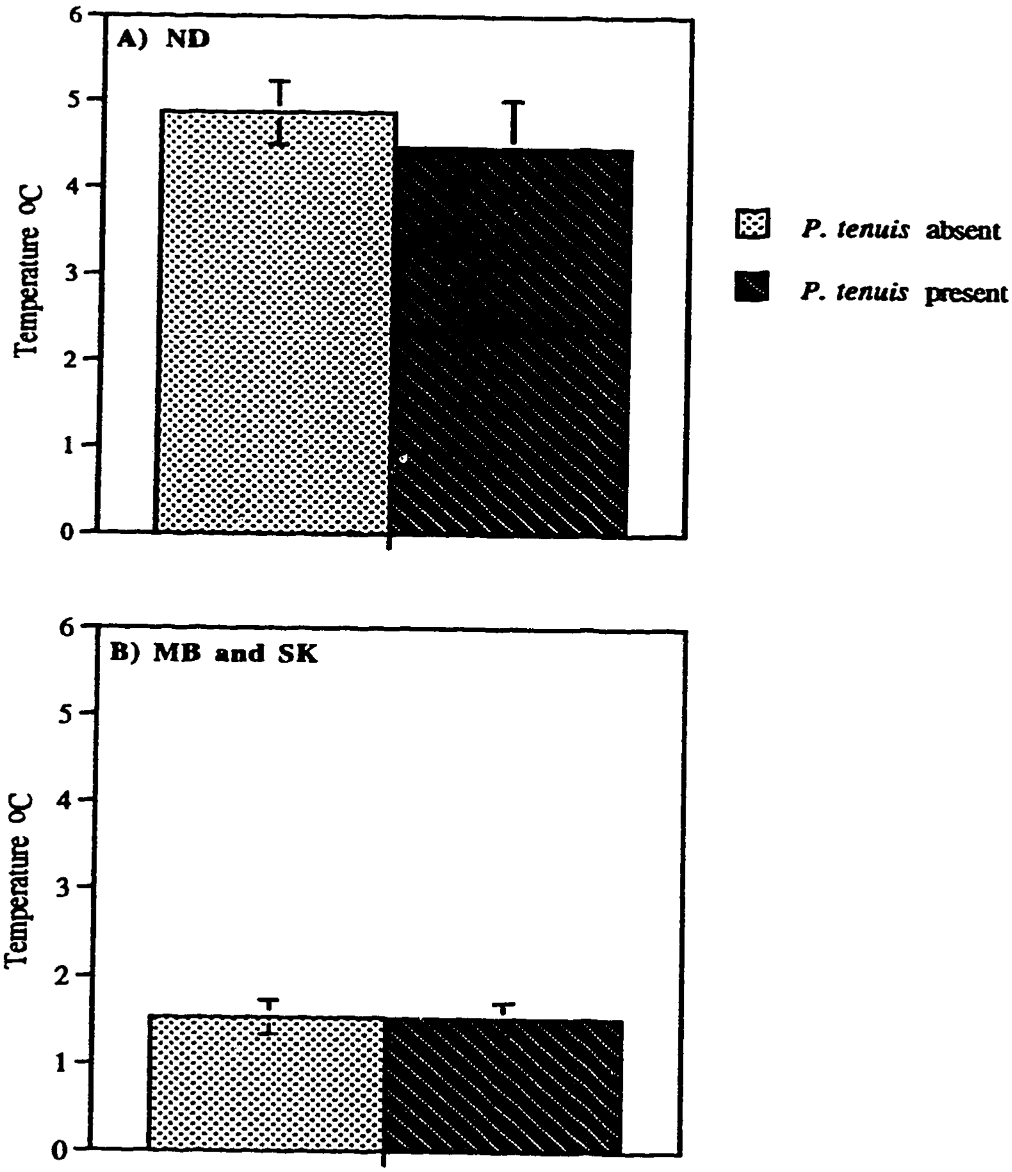


Figure 13. Mean normal (1951-1980) annual temperature (and standard errors) for all deer management units sampled in North Dakota (A), Manitoba and Saskatchewan (B) with *Parelaphostrongylus tenuis* present (n = 11 and 22, respectively) and deer management units with *P. tenuis* absent (n = 20 and 53, respectively).

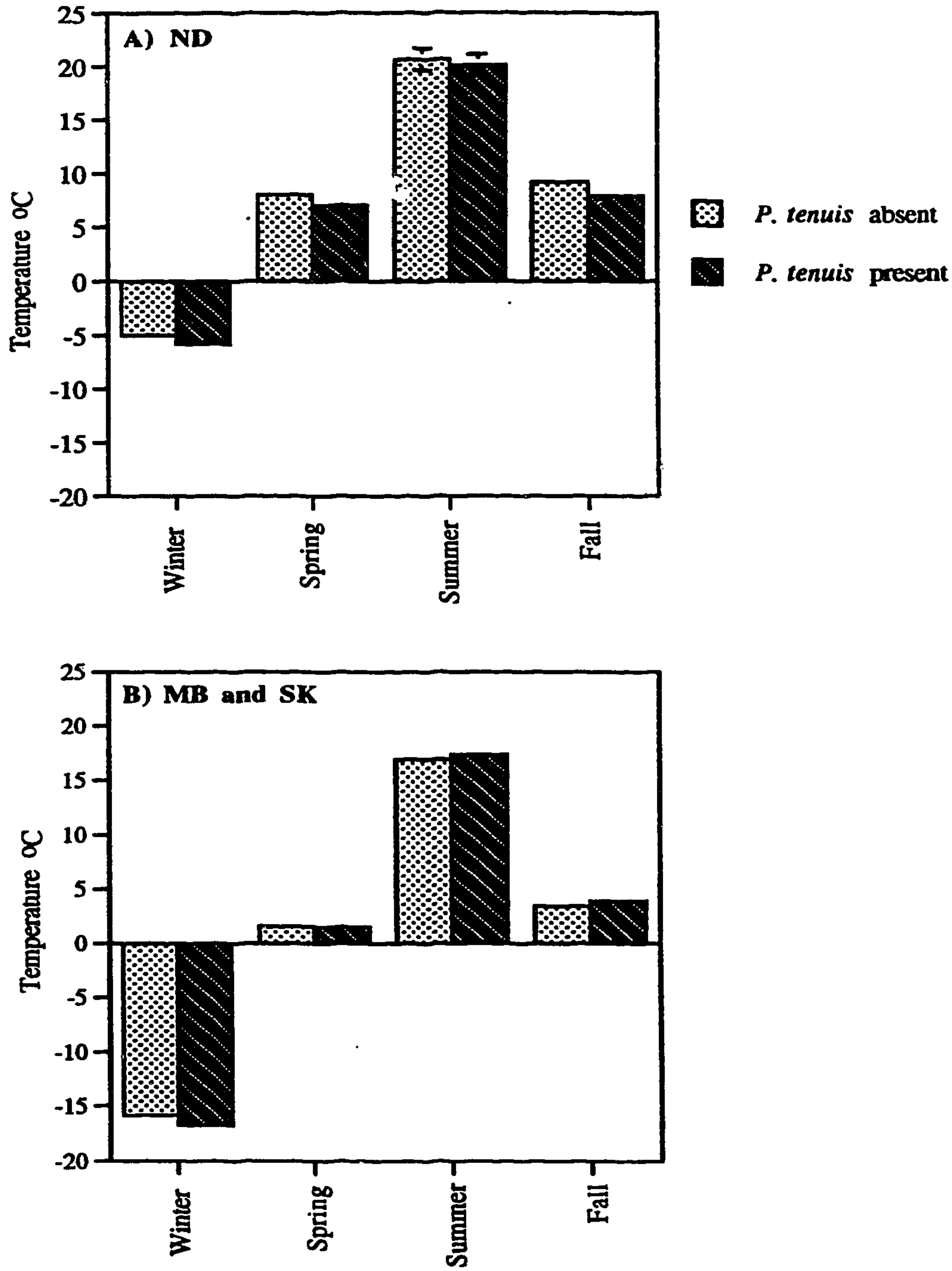


Figure 14. Mean winter (December, January, February), spring (March, April, May), summer (June, July, August), and fall (September, October, November) temperature (and standard errors) for all deer management units sampled in North Dakota (A) and Manitoba and Saskatchewan (B) with *Parelaphostrongylus tenuis* present (n = 11 and 22, respectively) and *P. tenuis* absent (n = 20 and 53, respectively).

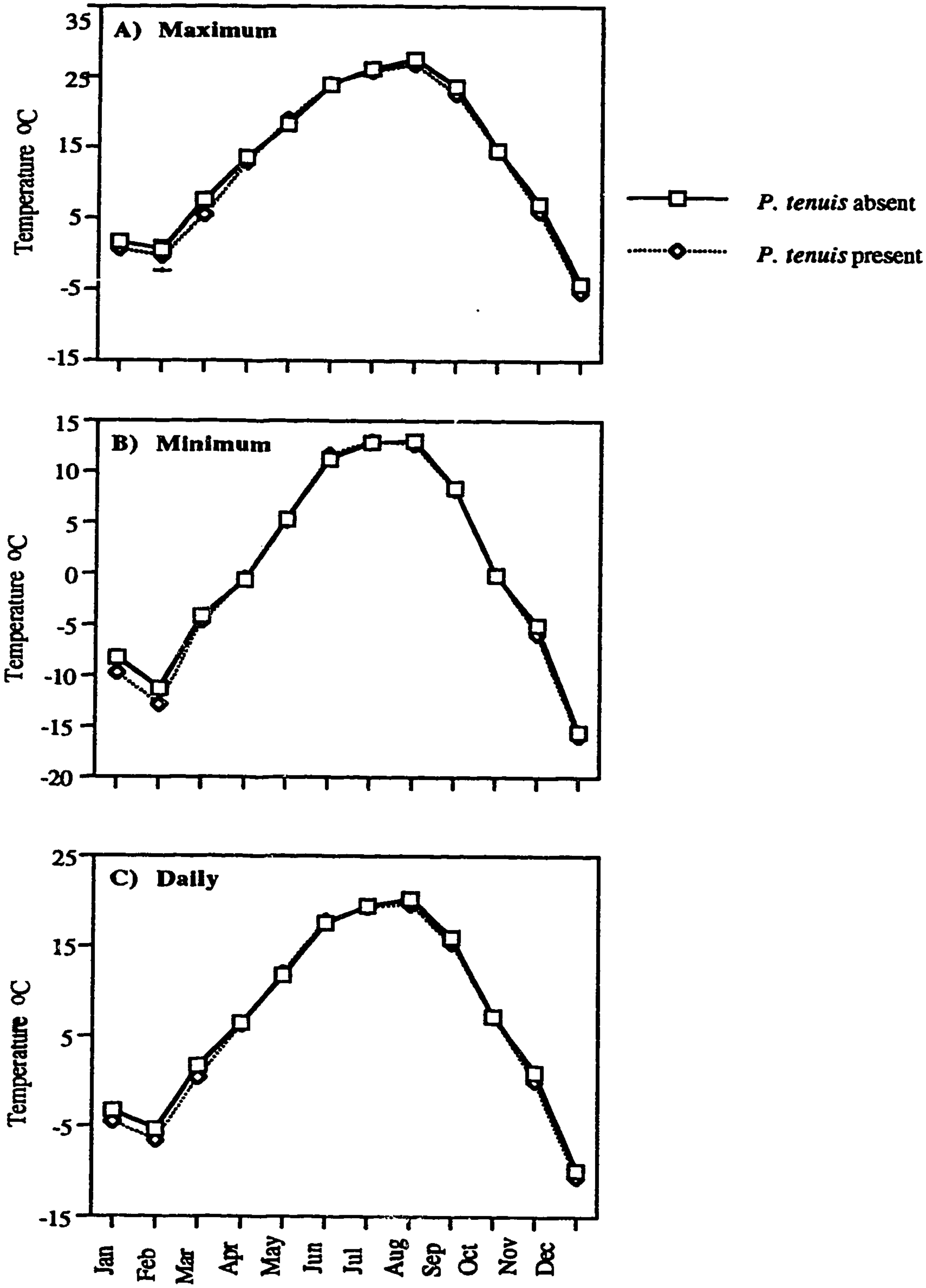


Figure 15. Mean normal (1951-1980) daily maximum (A), daily minimum (B), and daily average (C) temperature (and standard errors) for all deer management units sampled in North Dakota with *Parelaphostrongylus tenuis* present (n = 11) and *P. tenuis* absent (n = 20).

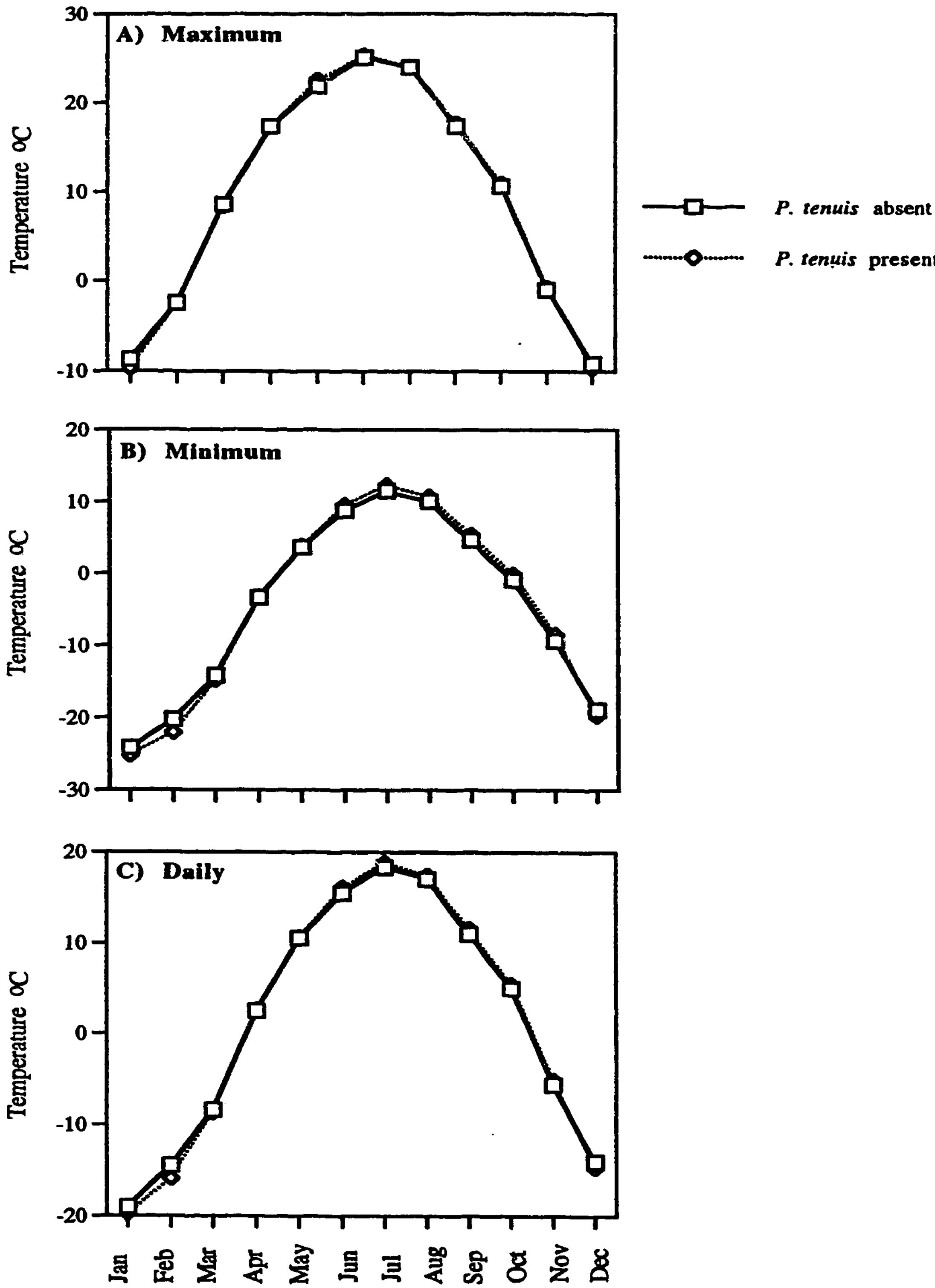


Figure 16. Mean normal (1951-1980) daily maximum (A), daily minimum (B), and daily average (C) temperature (and standard errors) for deer management units sampled in Manitoba and Saskatchewan with *Parelaphostrongylus tenuis* present (n = 22) and *P. tenuis* absent (n = 53).

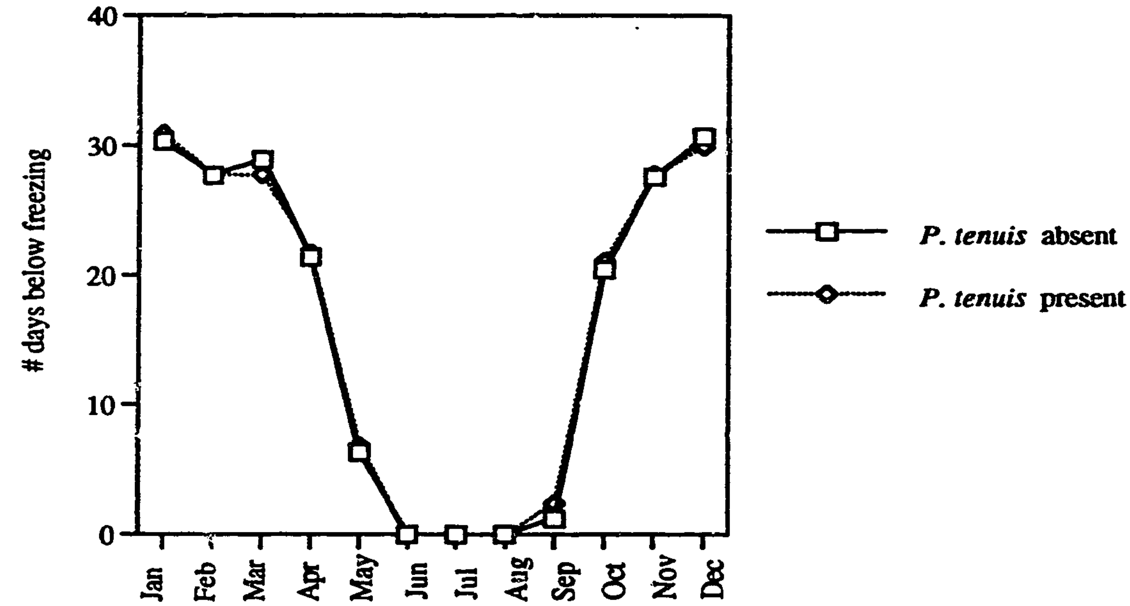


Figure 17. Mean number of days below freezing (and standard errors) for all deer management units sampled in North Dakota with *Parelaphostrongylus tenuis* present (n = 11) and *P. tenuis* absent (n = 20).

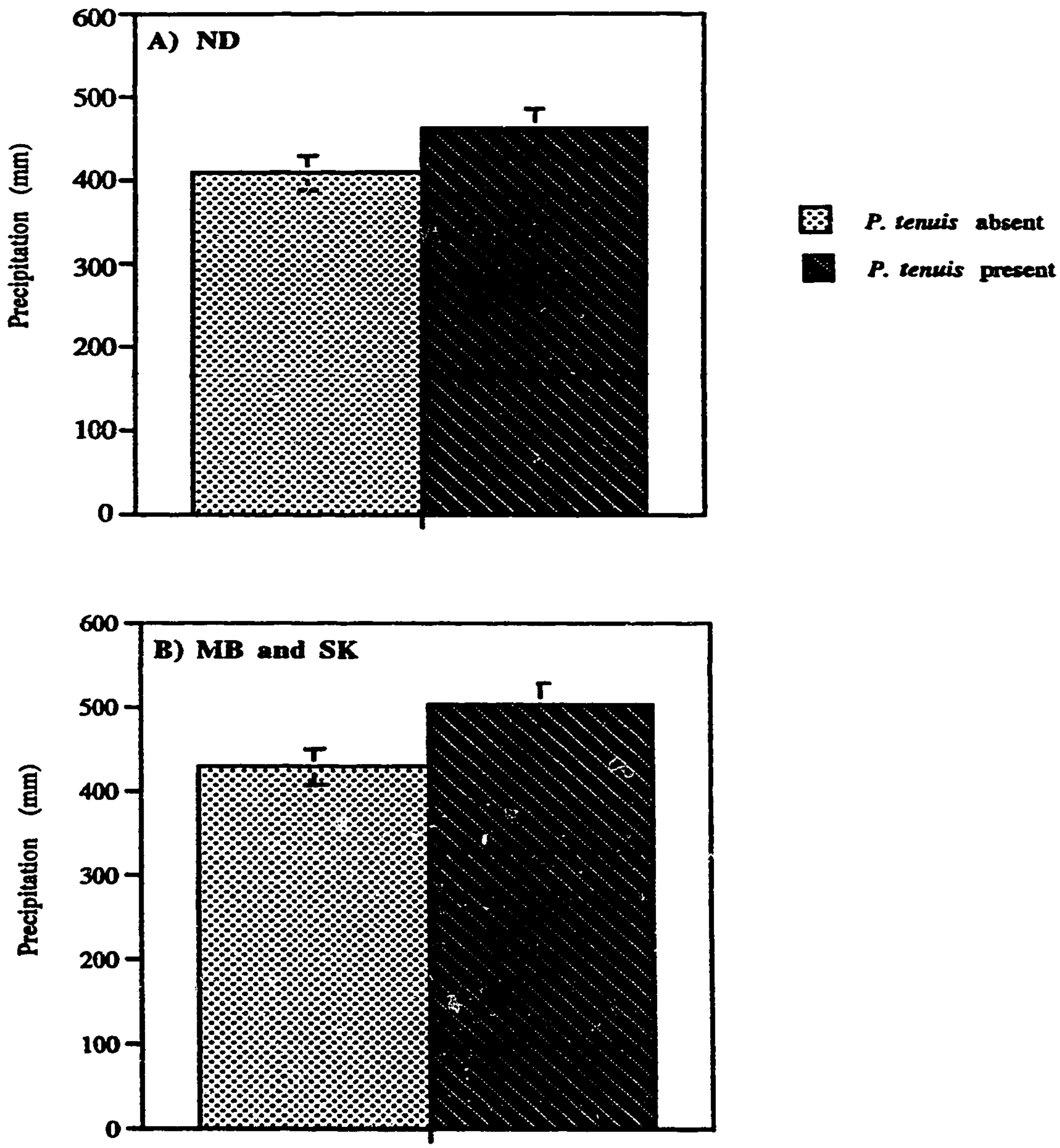


Figure 18. Mean normal (1951-1980) annual precipitation (and standard errors) for all deer management units sampled in North Dakota (A) and Manitoba and Saskatchewan (B) with *Parelaphostrongylus tenuis* present (n = 11 and 22, respectively) and with *P. tenuis* absent (n = 20 and 53, respectively).

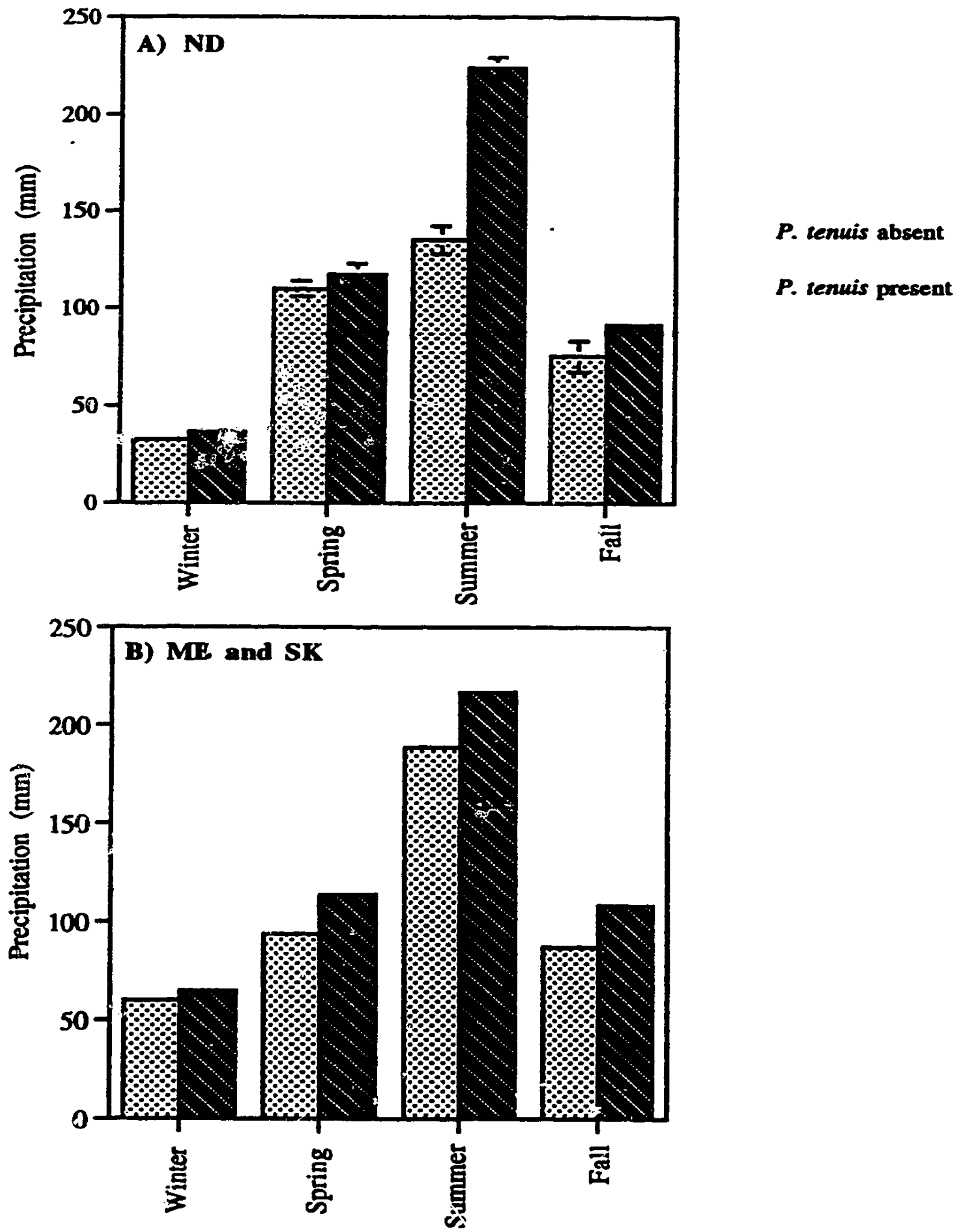


Figure 19. Mean winter (December, January, February), spring (March, April, May), summer (June, July, August), and fall (September, October, November) precipitation (and standard errors) for all deer management units sampled in North Dakota (A) and Manitoba and Saskatchewan (B) with *Parelaphostrongylus tenuis* present (n = 11 and 22, respectively) and *P. tenuis* absent (n = 20 and 53, respectively).

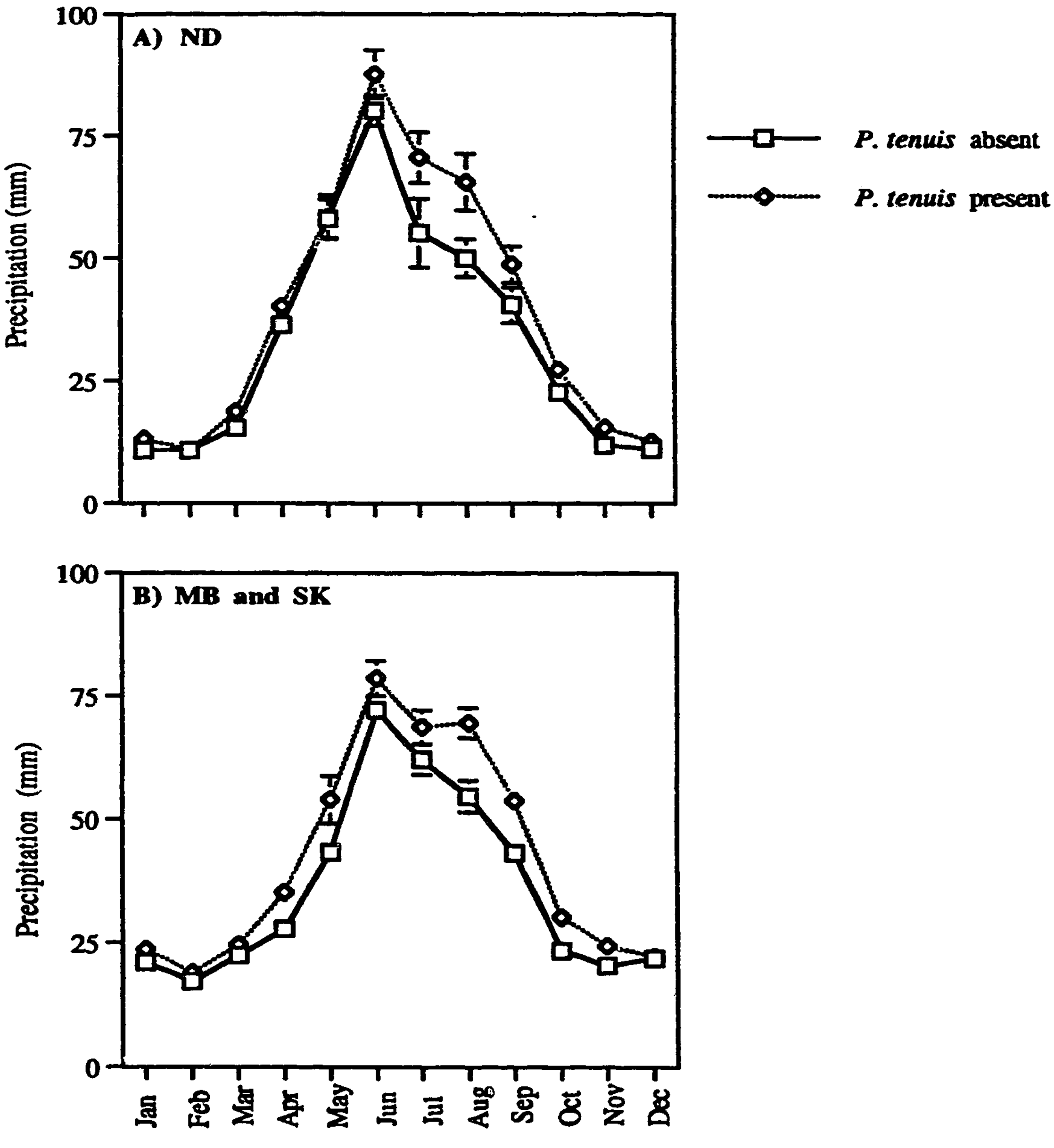


Figure 20. Mean normal (1951-1980) monthly precipitation (and standard errors) for all deer management units sampled in North Dakota (A), and Manitoba and Saskatchewan (B) with *Parelaphostrongylus tenuis* present (n = 11 and 22, respectively) and absent (n = 20 and 53, respectively).

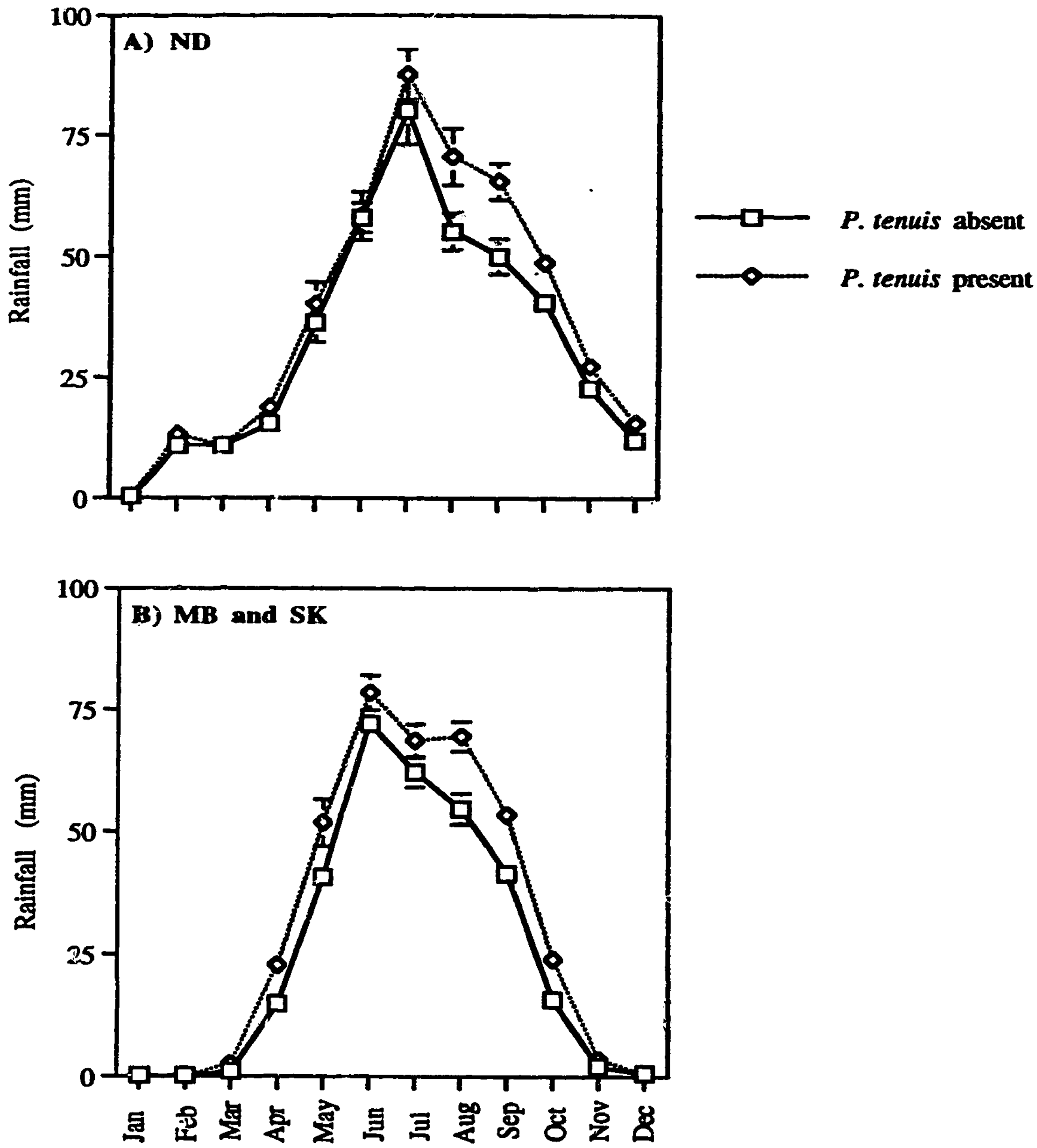


Figure 21. Mean normal (1951-1980) monthly rainfall (and standard errors) for deer management units sampled in (A) North Dakota and (B) Manitoba and Saskatchewan with *Parelaphostrongylus tenuis* present (n =11 and 22, respectively) and *P. tenuis* absent (n = 20 and 53, respectively).

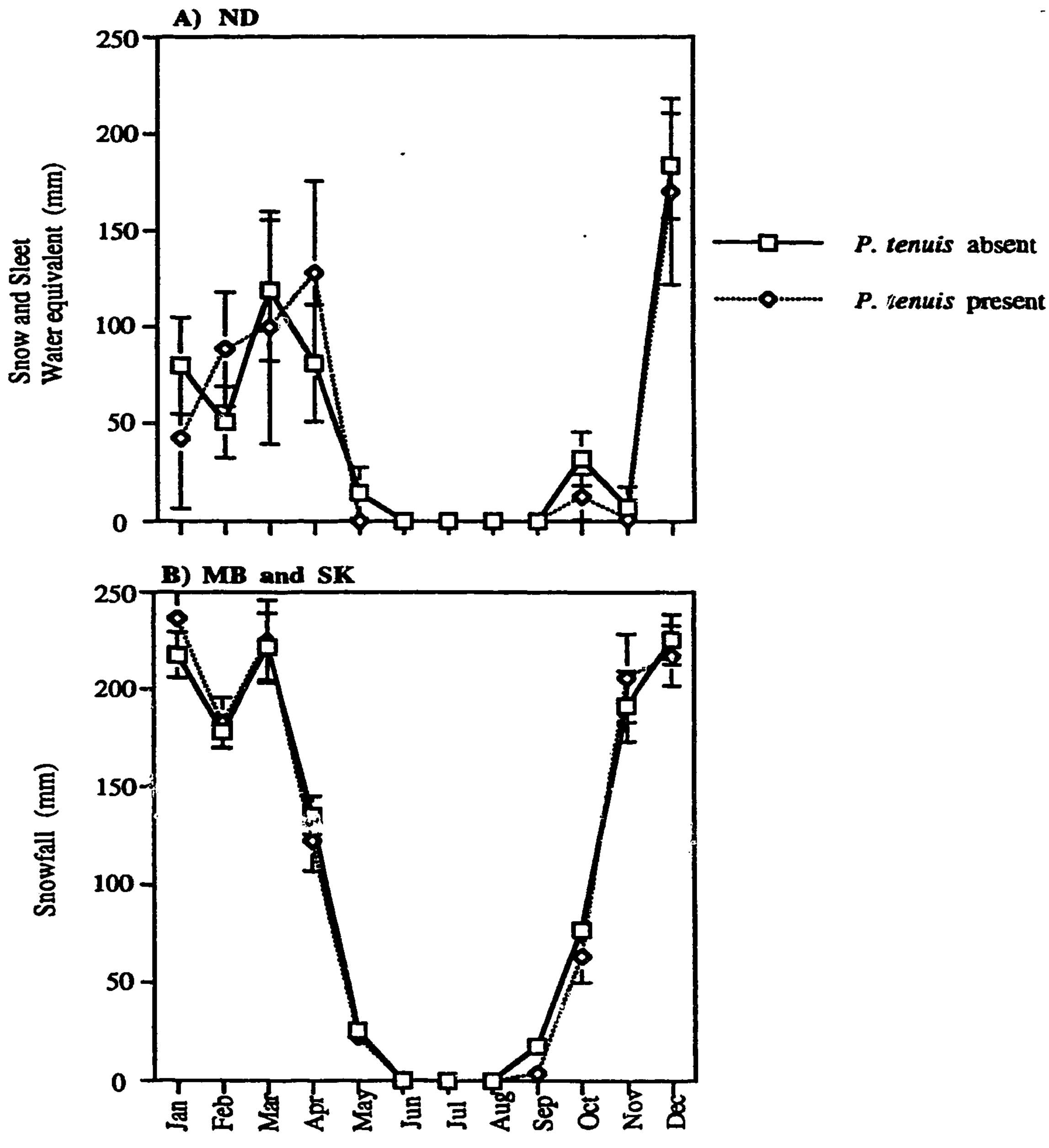


Figure 22. Mean normal (1951-1980) monthly sleet and snowfall (and standard errors) for deer management units sampled in (A) North Dakota and (B) Manitoba and Saskatchewan with *Parelaphostrongylus tenuis* present (n = 11 and 22, respectively) and *P. tenuis* absent (n = 20 and 53, respectively).

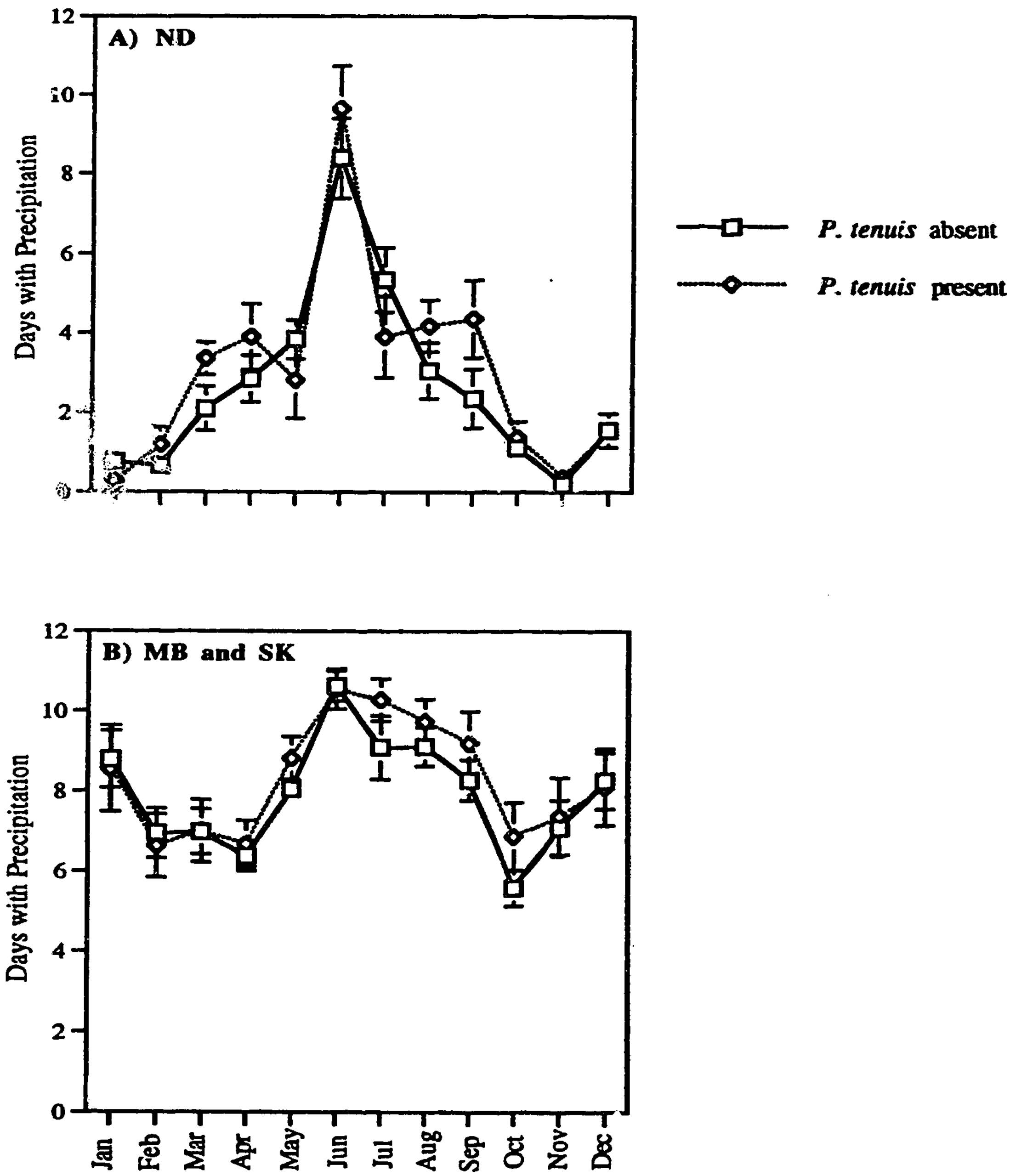


Figure 23. Normal (1951-1980) number of days with precipitation* (and standard errors) for deer management units sampled in North Dakota (A), and Manitoba and Saskatchewan (B) with *Parelaphostrongylus tenuis* present (n = 11 and 22, respectively) and deer management units with *P. tenuis* absent (n = 20 and 53, respectively).

* ≥ 0.2 mm rain or ≥ 2.0 mm snow for MB and SK, ≥ 2.5mm water equivalent for ND.

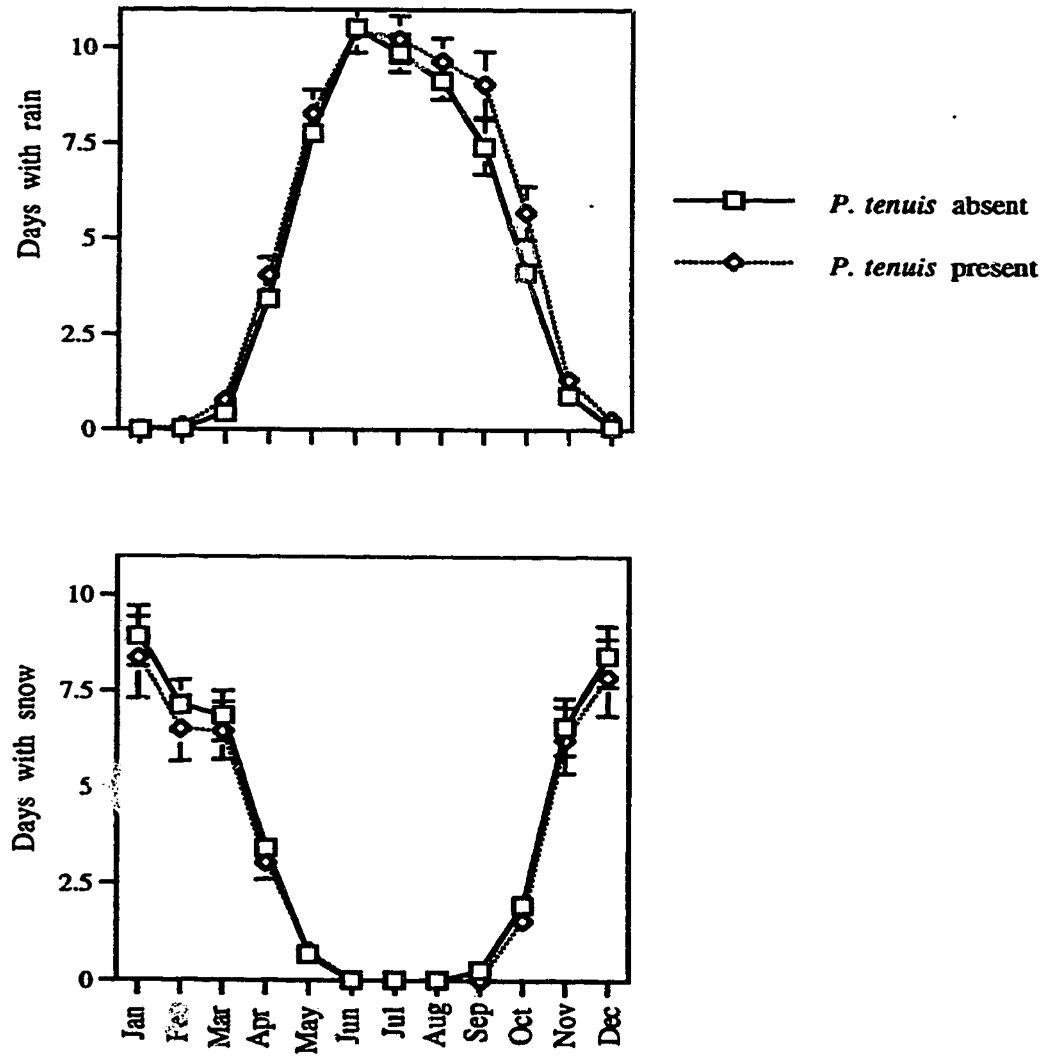


Figure 24. Normal (1951-1980) number of days with ≥ 0.2 mm rain or snow (and standard errors) for deer management units sampled in Manitoba and Saskatchewan with *Parelaphostrongylus tenuis* present (n = 22) and *P. tenuis* absent (n = 53).

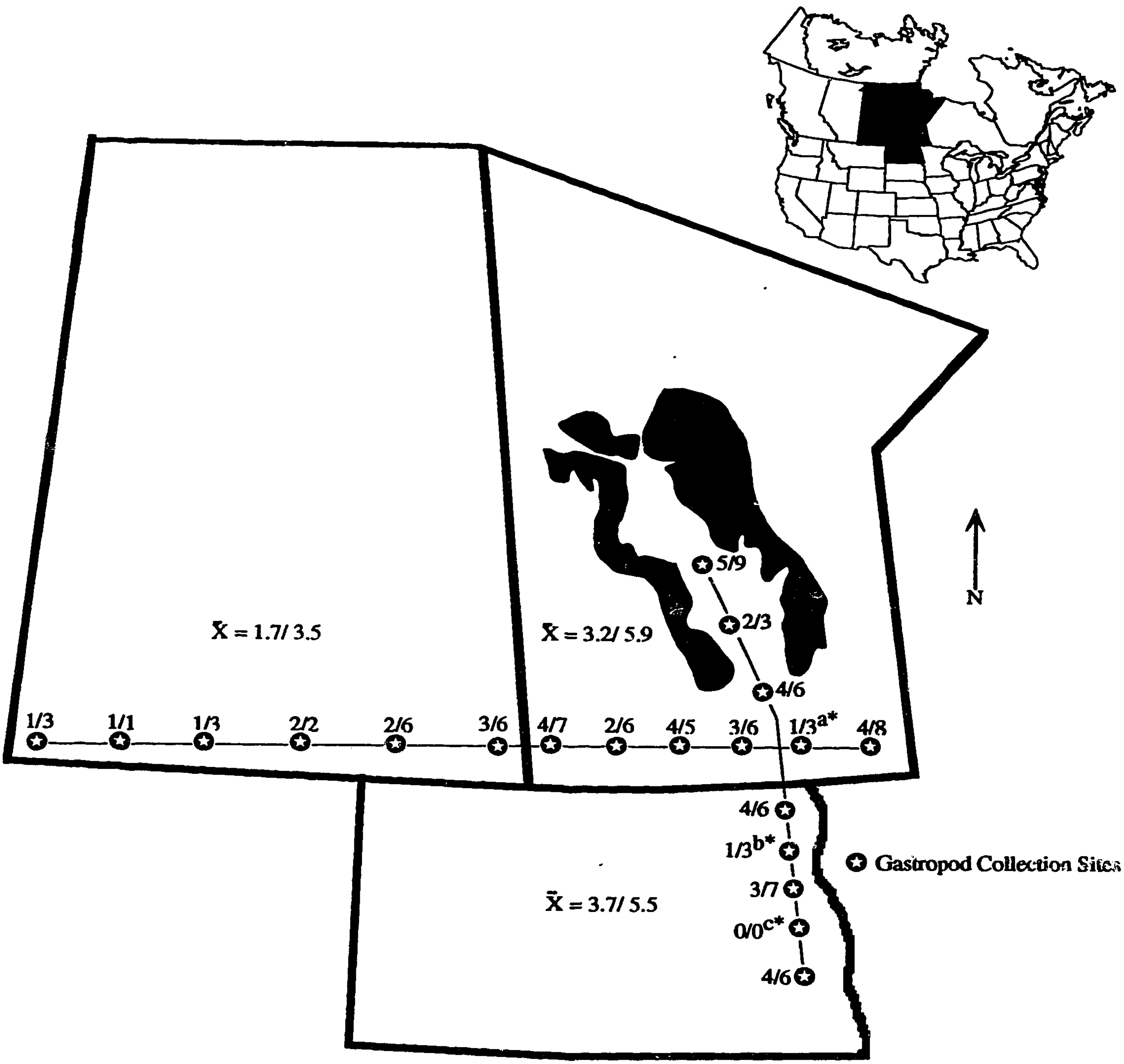


Figure 25. Sites where gastropods were collected in Saskatchewan, Manitoba, and North Dakota. Shown is the number of gastropod species that are known hosts of *Parelaphostrongylus tenuis*/ number of all gastropod species recovered at each site. Three sites (a, b, c) were defined as suboptimal. Not to scale.
* not included in means.

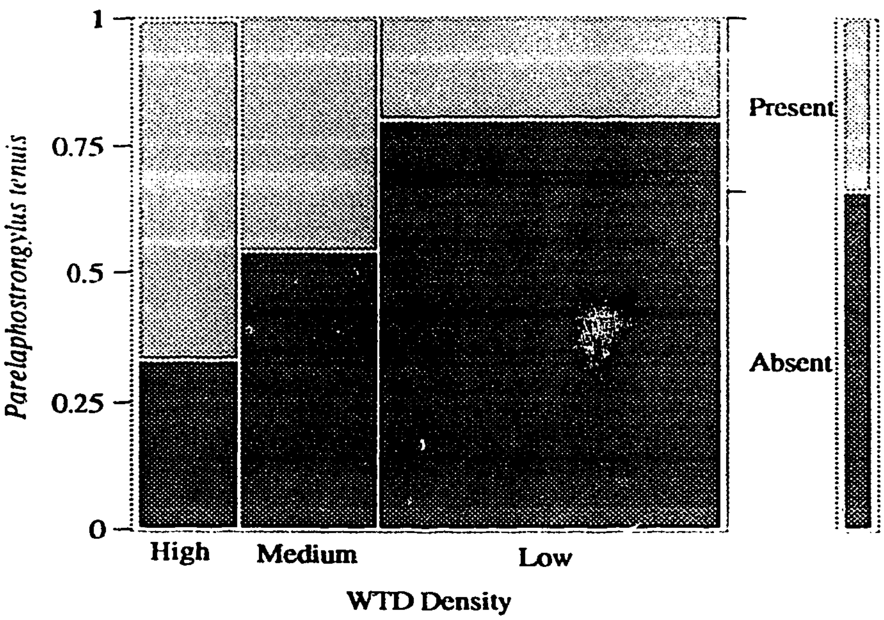


Figure 26. Univariate nominal logistic regression of white-tailed deer density versus presence or absence of *Parelaphostrongylus tenuis* for all deer management units sampled in North Dakota, Manitoba, and Saskatchewan (n = 89*/106). Low < 0.37/ km^2; Medium = 0.37-1.1/ km^2; High > 1.1/ km^2
* data were not available for 17 deer management units.

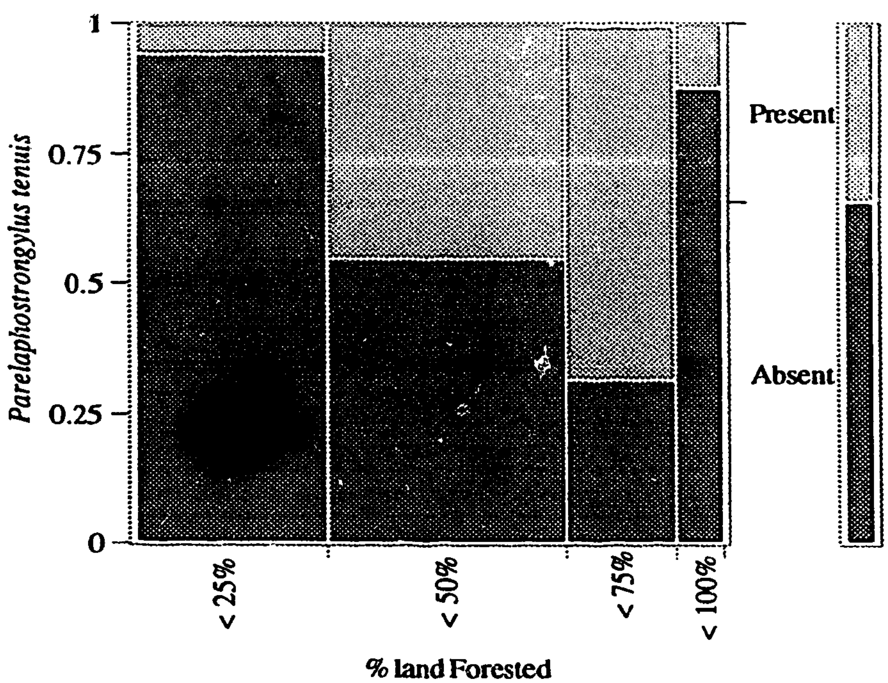


Figure 27. Univariate nominal logistic regression of % forested land versus presence or absence of *Parelaphostrongylus tenuis* for all deer management units sampled in North Dakota; Manitoba, and Saskatchewan (n = 89*/106).
* data were not available for 17 deer management units.

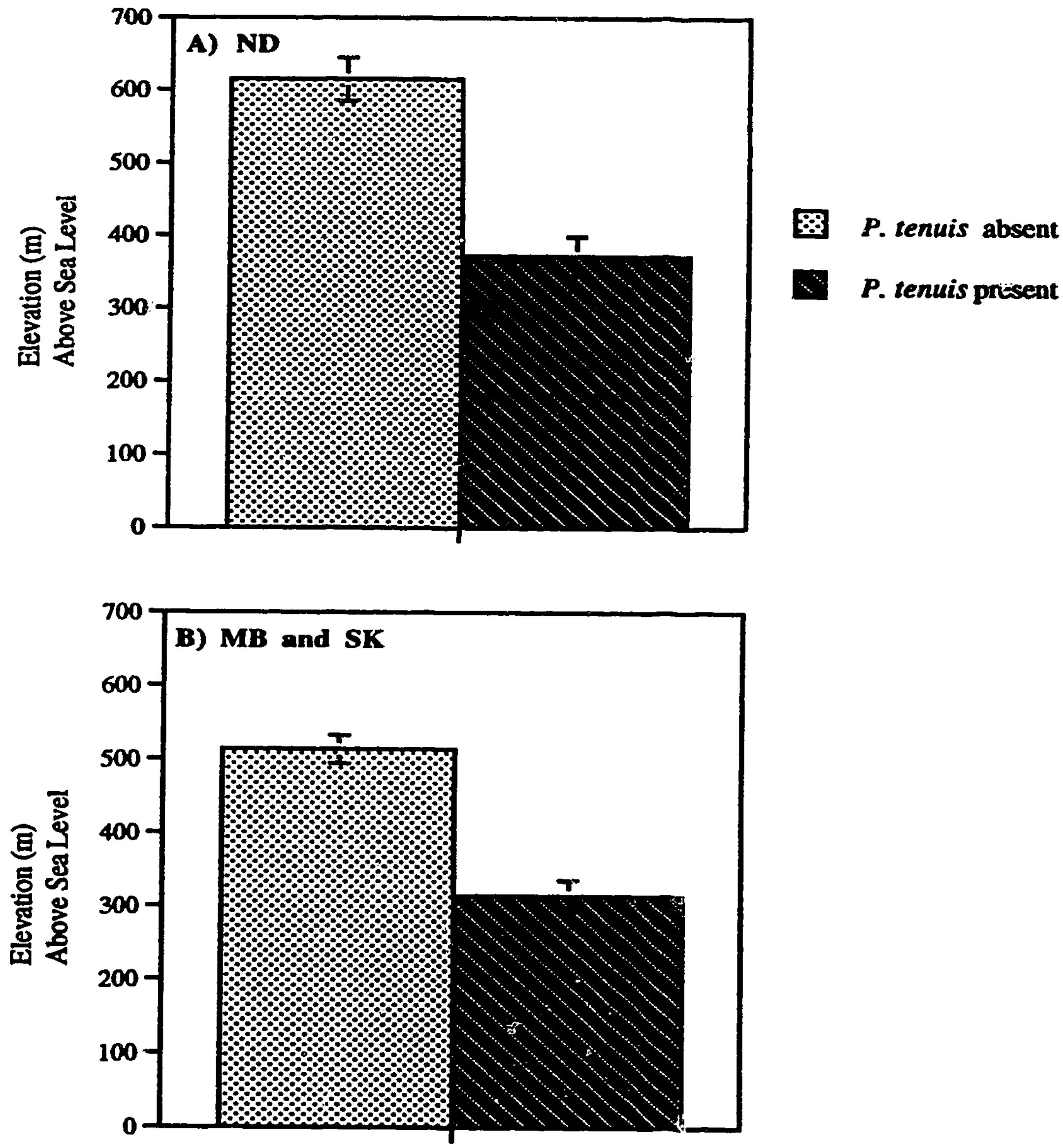
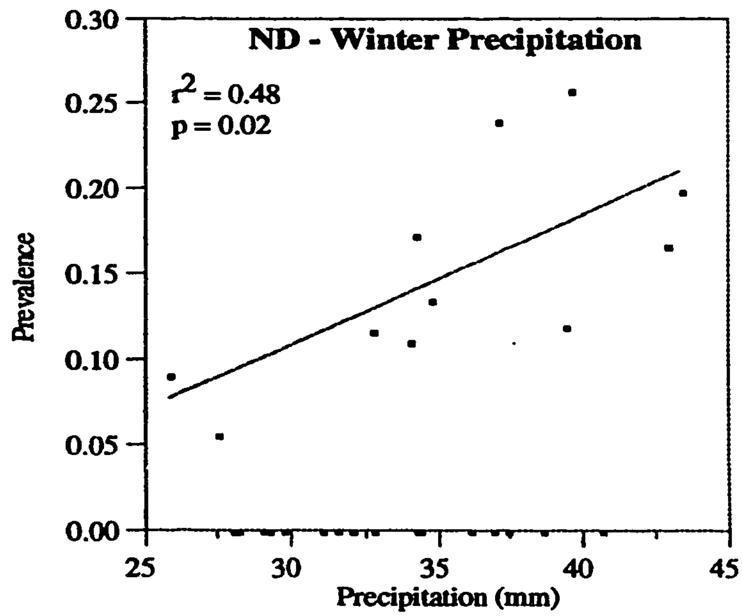


Figure 28. Mean elevation (and standard errors) for all deer management units sampled in North Dakota (A) and Manitoba and Saskatchewan (B) with *Parelaphostrongylus tenuis* present (n = 11 and 22, respectively) and deer management units with *P. tenuis* absent (n = 20 and 53, respectively).



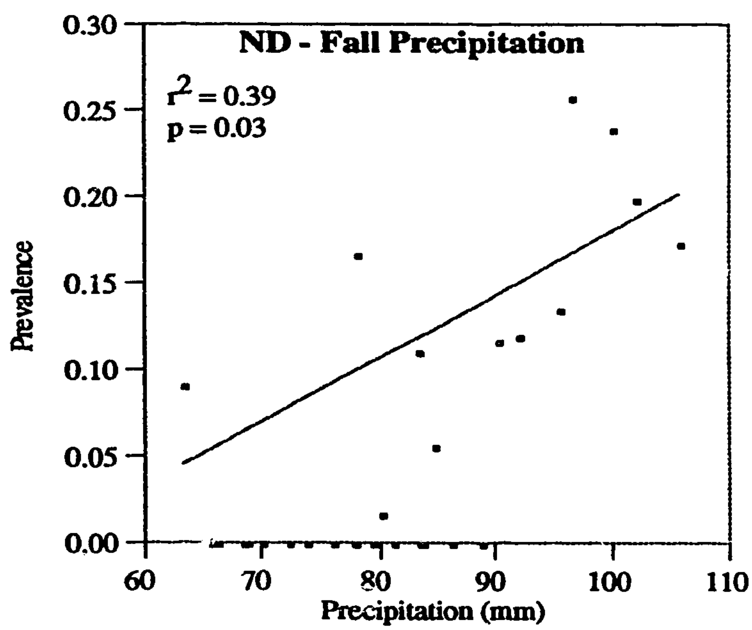


Figure 29. Linear regression analysis of seasonal precipitation and prevalence of *Parelaphostrongylus tenuis* infections (prevalence values = 0 not included in analysis).

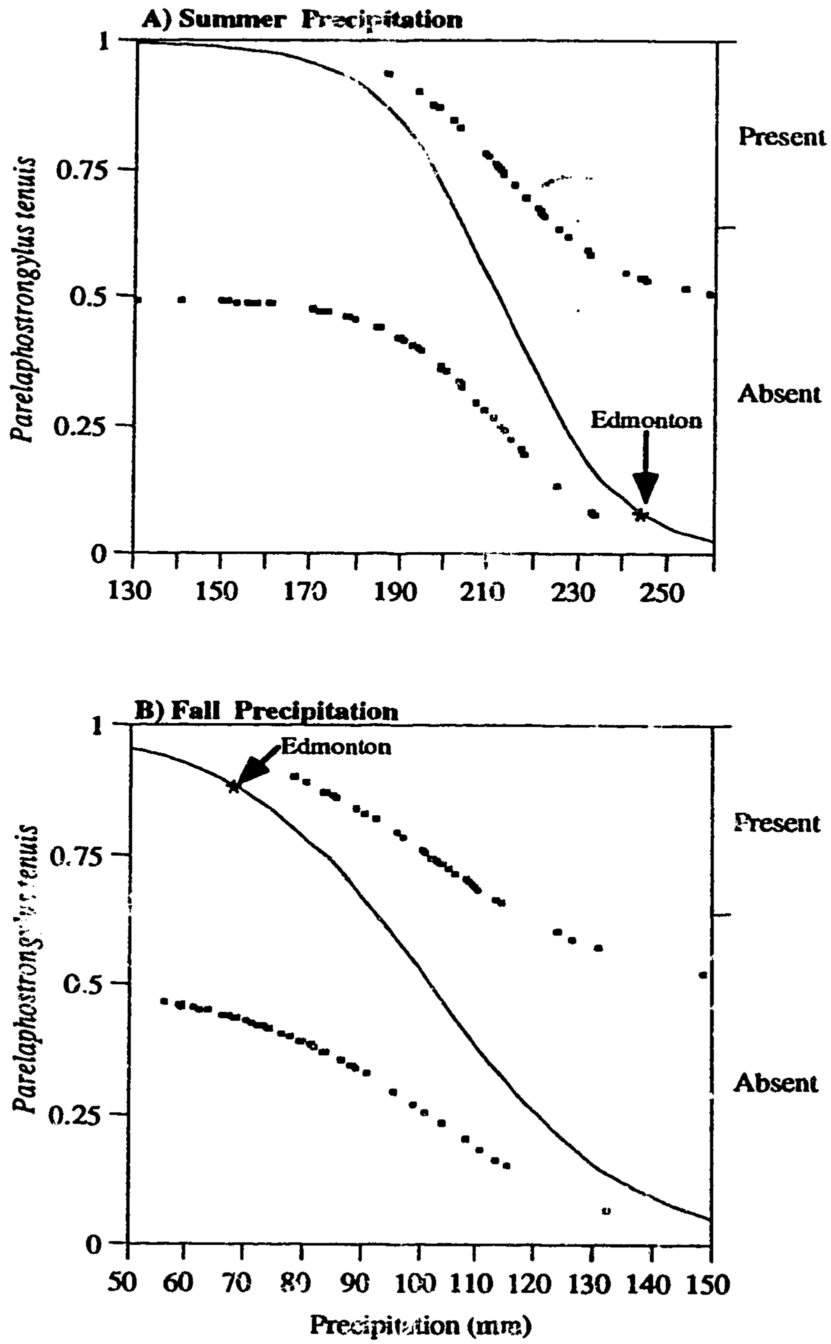


Figure 30. Univariate nominal logistic regression of summer (A) and fall (B) precipitation versus presence or absence of *Parelaphostrongylus tenuis* for all deer management units sampled in North Dakota, Manitoba, and Saskatchewan (n = 89*/106).
* data were not available for 17 deer management units.

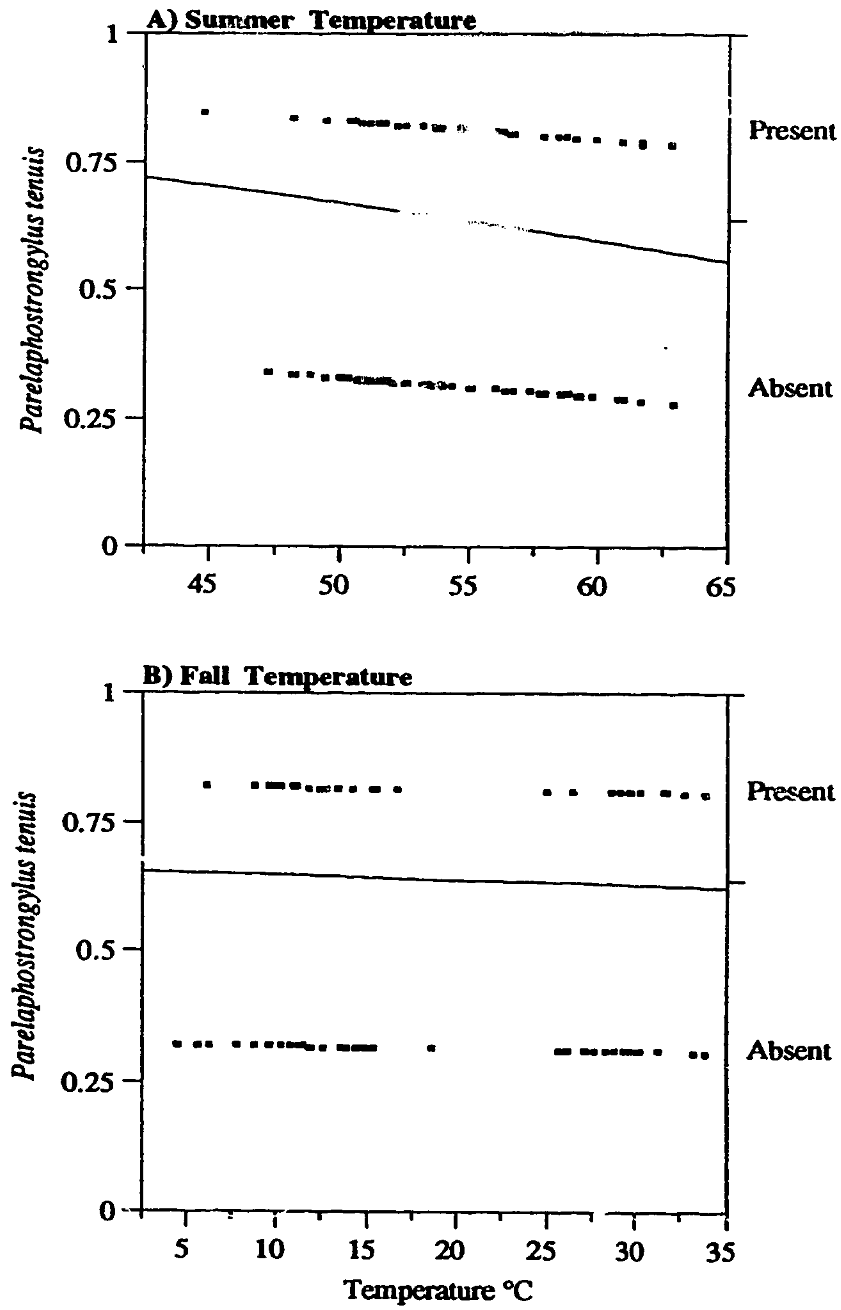


Figure 31. Univariate nominal logistic regression of summer (A) and fall (B) cumulative temperature versus presence or absence of *Parelaphostrongylus tenuis* for all deer management units sampled in North Dakota, Manitoba, and Saskatchewan (n = 89*/106).
* data were not available for 17 deer management units.

Literature Cited

Alden, C., F. Woodson, R. Mohan, and S. Miller. 1975. Cerebrospinal nematodiasis in sheep. Journal of the American Veterinary Medical Association 166: 784-786.

Alibasoglu, M., D.C. Kradel, and H.W. Dunne. 1961. Cerebral nematodiasis in Pennsylvania deer (*Odocoileus virginianus*). Cornell Veterinarian 51: 431-441.

Anderson, R.C. 1956. *Elaphostrongylus odocoilei* Hobmaier and Hobmaier, 1934 in the cranial case of *Odocoileus virginianus borealis* Miller. Canadian Journal of Zoology 34: 167-173.

Anderson, R.C. 1963a. The incidence, development, and experimental transmission of *Pneumostrongylus tenuis* Dougherty (Metastrongyloidea: Protostrongylidae) of the meninges of the white-tailed deer (*Odocoileus virginianus borealis*) in Ontario. Canadian Journal of Zoology 41: 775-792

Anderson, R.C. 1963b. Studies on *Pneumostrongylus tenuis* Dougherty, 1945 of *Odocoileus virginianus*. The Journal of Parasitology 49: 40-47.

Anderson, R.C. 1964. Neurologic disease in moose infected experimentally with *Pneumostrongylus tenuis* from white-tailed deer. Veterinary Pathology 1: 289-322.

Anderson, R.C. 1965a. An examination of moose exhibiting neurological signs, in Ontario. Canadian Journal of Zoology 43: 635-639.

Anderson, R.C. 1965b. The development of *Pneumostrongylus tenuis* in the central nervous system of white-tailed deer. Pathologia veterinaria 2: 360-379.

Anderson, R.C. 1972. The ecological relationships of meningeal worm and native cervids in North America. Journal of Wildlife Diseases 8: 304-310.

Anderson, R.C. 1992. Nematode Parasites of Vertebrates: Their Development and Transmission. C.A.B. International, University Press, Cambridge. 578pp.

Anderson, R.C., and U.R. Strelive. 1966. Experimental cerebrospinal nematodiasis (*Pneumostrongylus tenuis*) in sheep. Canadian Journal of Zoology 44: 889-894.

Anderson, R.C., and U.R. Strelive. 1967. The penetration of *Pneumostrongylus tenuis* into the tissues of white-tailed deer. Canadian Journal of Zoology 45: 285-289.

Anderson, R.C., and U.R. Strelive. 1968. The experimental transmission of *Pneumostrongylus tenuis* to caribou (*Rangifer tarandus terraenovae*). Canadian Journal of Zoology 46: 503-510.

Anderson, R.C., and A.K. Prestwood. 1981. Lungworms. *In* Davidson, W.R., F.A. Hayes, V.F. Nettles, and F.E. Kellogg (eds.) Diseases and parasites of white-tailed deer. Miscellaneous Publications Number 7, Tall Timbers Research Station, Tallahassee, FL. pp. 266-317.

Anderson, R.C., M.W. Lankester, and U.R. Strelive. 1966. Further experimental studies of *Pneumostrongylus tenuis* in cervids. Canadian Journal of Zoology 44: 851-861.

Anonyomous. 1980. Canadian Climate Normals 1951-1980. Prairie Provinces. Canadian Climate Center; Environment Canada, Atmospheric Environment Service. Downsview, Ontario.

Anonyomous. 1989a. Climatological Station Catologue. Environment Canada, Atmospheric Environment Service. Downsview, Ontario.

Anonyomous. 1989b. Climatological Data. North Dakota. National Oceanic and Atmospheric Administration. Vol. 98, Nos. 1 - 13.

Anonyomous. 1990. Climatological Data. North Dakota. National Oceanic and Atmospheric Administration. Vol. 99, Nos. 1 - 13.

Baumgartner, W., A.M. Zodiac, B/L. Hull, F. Andrews, and F. Gar. 1985. Parelaphostrongylosis in llamas. Journal of the American Veterinary and Medical Association 187: 1243-1245.

Beaudoin, R.L., W.M. Samuel, and C.P.A. Strome. 1970. A comparative study of the parasites in two populations of white-tailed deer. Journal of Wildlife Diseases 6: 56-63.

Behrend, D.F. 1970. The nematode, *Pneumostrongylus tenuis*, in white-tailed deer in the Adirondacks. New York Fish and Game Journal 17: 45-49.

Behrend, D.F., and J.F. Witter. 1968. *Pneumostrongylus tenuis* in white-tailed deer in Maine. Journal of Wildlife Management 32: 963-966.

Bergerud, A.T., and W.E. Mercer. 1989. Caribou introductions in eastern North America. Wildlife Society Bulletin 17: 111-120.

Bindernagel, J.A., and R.C. Anderson. 1972. Distribution of the meningeal worm in white-tailed deer in Canada. Journal of Wildlife Manangement 36: 1349-1353.

Boag, D.A. 1990. On the effectiveness of artificial shelters in the study of population attributes of small terrestrial gastropods. Canadian Journal of Zoology 68: 254-262.

Bogaczyk, B.A., W.B. Krohn, and H.C. Gibbs. 1993. Factors affecting *Parelaphostrongylus tenuis* in white-tailed deer (*Odocoileus virginianus*) from Maine. Journal of Wildlife Diseases 29: 266-272.

Brown, T.T., Jr., H.E. Jordan, and C.N. Demorest. 1978. Cerebrospinal parelaphostrongylosis in llamas. Journal of Wildlife Diseases 14: 441-444.

Bruijns, M.F.M., C.O. Van Regteren Altena, and L.J.M. Butot. 1959. The Netherlands as an Environment for Land Mollusca. Basteria 23: 132-162.

Burch, J.B. 1956. Distribution of land snails in plant associations in eastern Virginia. Nautilus. 70: 60-64

Burch, J. B. 1962. How to know the eastern land snails. William C. Brown Co., Dubuque, Iowa

Carlsen, J.C., and R.E. Farmes. 1957. Movements of white-tailed deer tagged in Minnesota. The Journal of Wildlife Management. 21: 397-401

Carpenter, J.W., H.E. Jordan, and J.A. Morrison. 1972. Meningeal worm (*Parelaphostrongylus tenuis*) infection in white-tailed deer in Oklahoma. Journal of Wildlife Diseases 8: 381-383.

Carpenter, J.W., H.E. Jordan, and B.C. Ward. 1973. Neurologic disease in wapiti naturally infected with meningeal worms. Journal of Wildlife Diseases 9: 148-153.

Clarke, A.H., Jr., J.P. Kelsall, and G.R. Parker. 1968. The Land Snail Fauna of Fundy National Park, New Brunswick. National Museum of Canada. Contrib. Zool. 4 Bull. 223: 5-22

Comer, J.A., W.R. Davidson, A.K. Prestwood, and V.F. Nettles. 1991. An update on the distribution of *Parelaphostrongylus tenuis* in the southeastern United States. Journal of Wildlife Diseases 27: 348-354.

Dauphine, T.C., Jr. 1975. The disappearance of caribou reintroduced to Cape Breton Highlands National Park. Canadian Field-Naturalist 89: 299-310.

Davidson, W.R., J.M. Crum, J.L. Blue, D.W. Sharp, and J.H. Phillips. 1985. Parasites, diseases, and health status of sympatric populations of fallow deer and white-tailed deer in Kentucky. Journal of Wildlife Diseases 21: 153-159.

DeGiusti, D.L. 1955. The occurrence of a protostrongylid nematode in the meninges of Michigan deer. The Journal of Parasitology 41(2): 42

DeGiusti, D.L. 1963. Incidence and distribution of *Elaphostrongylus odocoilei* in Michigan deer herd. The Journal of Parasitology 49 (Suppl.): 47

Dew, T.L. 1988. Prevalence of *Parelaphostrongylus tenuis* in a sample of hunter-harvested white-tailed deer from a tri-county area in northeastern Wisconsin. Journal of Wildlife Diseases 24: 720-721.

Dew, T.L., D.D. Bowman, and R.B. Grieve. 1992. Parasite-specific immunoglobulin in the serum and cerebrospinal fluid of white-tailed deer (Odocoileus virginianus) and goats (Capra hircus) with experimentally induced parelaphostrongylosis. Journal of Zoo and Wildlife Medicine 23: 281-287.

Dudak, D., G.W. Cornwell, R.B. Holliman, and B.S. McGinnes. 1965. The incidence and degree of infection of *Pneumostrongylus tenuis* in the white-tailed deer of western Virginia. Transactions of the Annual Conference of the Southeastern Association of the Game and Fish Commissioners, Tulsa, OK 19: 128-141.

Eckroade, R.J., G.M. ZuRhein, M. Gabriele, and W. Foreyt. 1970. Meningeal worm invasion of the brain of a naturally infected white-tailed deer. Journal of Wildlife Diseases 6: 430-436.

Foreyt, W.J., and B.B. Compton. 1991. Survey for meningeal worm (*Parelaphostrongylus tenuis*) and ear mites in white-tailed deer from northern Idaho. Journal of Wildlife Diseases 27: 716-718.

Forrester, D.J. 1992. *In* Parasites and diseases of wild mammals in Florida. University Press of Florida, Gainesville, FL. 459pp.

Garner, D.L., and W.F. Porter. 1991. Prevalence of *Parelaphostrongylus tenuis* in white-tailed deer in northern New York. Journal of Wildlife Diseases 27: 594-598.

Gilbert, F.F. 1973. *Parelaphostrongylus tenuis* (Dougherty) in Maine: 1 - The parasite in white-tailed deer (*Odocoileus virginianus*, Zimmermann). Journal of Wildlife Diseases 9: 136-143.

Gray, J.B., W.M. Samuel, A.W. Shostak, and M.J. Pybus. 1985. *Varestrongylus alpenae* (Nematoda: Metastrongyloidea) in white-tailed deer (*Odocoileus virginianus*) of Saskatchewan. Canadian Journal of Zoology 63: 1449-1454.

Gregory, R.D. and T.M. Blackburn. 1991. Parasite prevalence and host sample size. Parasitology Today. 7: 11.

Guthery, F.S., S.L. Beasom, and L. Jones. 1979. Cerebrospinal nematodiasis caused by *Parelaphostrongylus tenuis* in Angora goats in Texas. Journal of Wildlife Diseases 15: 37-47.

Halvorsen, O., and R.M. Anderson. 1982. On the population biology of *Elaphostrongylus rangiferi* (Nematoda) in reindeer, *Rangifer tarandus tarandus*. Molecular Biochemical Parasitology supplement, p. 469.

Hawkins, R.E., W.D. Klimstra, and D.C. Autry. 1971. Dispersal of deer from Crab Orchard National Wildlife Refuge. The Journal of Wildlife Management 35: 216-220

Healy, M.J.R. 1987. Choice of Sample Size in Parasitological Experiments. Parasitology Today 3: 3.

Halfpenny, J.C. and R.D. Ozanne. 1989. Winter: An Ecological Handbook. Johnson Publishing Co. Boulder Colorado. USA.

Jarvinen, J.A., and W.A. Hedberg. 1993. *Parelaphostrongylus tenuis* (Nematoda) in white-tailed deer (*Odocoileus virginianus*) in central Iowa. The Journal of Parasitology 79: 116-119.

Jortner, B.S., H.F. Troutt, T. Collins, and K. Scarratt. 1985. Lesions of spinal cord parelaphostrongylosis in sheep. Sequential changes following intramedullary larval migration. Veterinary Pathology 22: 137-140.

Kahn, R. 1993. Wildlife management agency concerns about captive wildlife: The Colorado experience. Transactions North American Wildlife and Natural Resources Conference 58: 495-503.

Karns, P.D. 1967. *Pneumostrongylus tenuis* in deer in Minnesota and implications for moose. Journal of Wildlife Management 31: 299-303.

Kearney, S.R., and F.F. Gilbert. 1978. Terrestrial gastropods from the Himsworth Game Preserve, Ontario, and their significance in *Parelaphostrongylus tenuis* transmission. Canadian Journal of Zoology 56: 688-694.

Kennedy, P.C., J.H. Whitlock, and S.J. Roberts. 1952. Neurofilariosis, a paralytic disease of sheep. I. Introduction symptomatology and pathology. Cornell Veterinarian 42: 118-124.

Kistner, T.P., G.R. Johnson, and G.A. Rilling. 1977. Naturally occurring neurologic disease in a fallow deer infected with meningeal worms. Journal of Wildlife Diseases 13: 55-58.

Kocan, A.A., M.G. Shaw, K.A. Waldrup, and G.J. Kubat. 1982. Distribution of *Parelaphostrongylus tenuis* (Nematoda: Metastrongyloidea) in white-tailed deer from Oklahoma. Journal of Wildlife Diseases 18: 457-460.

Kopcha, M, J.V. Marteniuk, R. Sills, B. Steficek, and T.W. Schillhorn van Veen. 1989. Cerebrospinal nematodiasis in a goat herd. Journal of the American Veterinary and Medical Association 194:1439-1442.

Krogdahl, D.W., J.P. Thilsted, and S.K. Olsen. 1987. Ataxia and hypermetria caused by Parelaphostrongylus tenuis infection in llamas. Journal of the American Veterinary and Medical Association 190:191-193.

Kurtz, H.J., K. Loken, and J.C. Schlotthauer. 1966. Histopathologic studies on cerebrospinal nematodiasis of moose in Minnesota naturally infected with *Pneumostrongylus tenuis.* American Journal of Veterinary Research 27: 548-558.

Lankester, M.W. 1974. *Parelaphostrongylus tenuis* (Nematoda) and *Fascioloides magna* (Trematoda) in moose of southeastern Manitoba. Canadian Journal of Zoology 52: 235-239.

Lankester, M.W., and R.C. Anderson. 1968. Gastropods as intermediate hosts of *Pneumostrongylus tenuis* Dougherty of white-tailed deer. Canadian Journal of Zoology 46: 373-383.

Locasciulli, O., and D.A. Boag. 1987. Microdistribution of terrestrial snails (Stylommatophora) in forest litter. Canadian Field Naturalist. 101: 76-81.

Loken, K.I., J.C. Schlotthauer, H.J. Kurtz, and P.D. Karns. 1965. *Pneumostrongylus tenuis* in Minnesota moose (*Alces alces*). Wildlife Disease Association Bulletin 1: 7.

Lunn, D.K., and K.W. Hinchcliff. 1989. Cerebrospinal fluid eosinophilia and ataxia in five llamas. Veterinary Record 124: 302-305.

Matson, G. M. 1981. Workbook for cementum analysis. Published by Matson. Milltown, MT.

Mayhew, I.G., A. deLahunta, J.R. Georgi, and D.G. Aspros. 1976. Naturally occurring cerebrospinal parelaphostrongylosis. Cornell Veterinarian 66: 56-72.

Maze, R.J., and C. Johnstone. 1986. Gastropod intermediate hosts of the meningeal worm *Parelaphostrongylus tenuis* in Pennsylvania: observations on their ecology. Canadian Journal of Zoology 64: 185-188.

Miller, M.W., and E.T. Thorne. 1993. Captive cervids as potential sources of disease for North America's wild cervid populations: avenues, implications and preventive management. Transactions North American Wildlife and Natural Resources Conference 58: 460-467.

Neilsen, S.W., and J. Aftosmis. 1964. Spinal nematodiasis in two sheep. Journal of the American Veterinary Medical Association 144: 155-158.

Nettles, V.F., A.K. Prestwood, R.G. Nichols, and C.J. Whitehead. 1977. Meningeal worm-induced neurologic disease in black-tailed deer. Journal of Wildlife Diseases 13: 137-143.

Nichols, D.K., R.J. Montali, M. Bush, L. Phillips, and L. Collins. 1986. Parelaphostrongylus tenuis infections in captive exotic ungulates. Proceedings of the Annual Meeting of the American Association of Zoo Veterinarians: 27-28.

Nixon, C.M., L.P. Hansen, P.A. Brewer, and J.E. Chelsvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. Wildlife Monographs 118.

O'Brien, T.D., T.P. O'Leary, J.R. Leininger, D.M. Sherman, D.L. Stevens, and C.B. Wolf. 1986. Cerebrospinal parelaphostrongylosis in Minnesota. Minnesota Veterinarian 26: 18-22.

Owen, W.B., Jr. 1974. A survey of the helminth parasites of white-tailed deer (*Odocoileus virginianus* Rafinesque) in five regions of Arkansas. Ph.D.. Thesis, University of Arkansas, Little Rock, 94pp.

Peterson, W.J., and M.W. Lankester. 1991. Aspects of the epizootiology of *Parelaphostrongylus tenuis* in a white-tailed deer population. Alces 27: 183-192.

Pilsbry, H.A. 1948. Land Mollusca of North America (north of Mexico). Vol. II. Parts 2 and 3. Monograph The Academy of Natural Sciences. Philadelphia. No. 3. pp. 521-113.

Platt, T.R. 1989. Gastropod intermediate hosts of *Parelaphostrongylus tenuis* (Nematoda: Metastrongyloidea) from northwestern Indiana. The Journal of Parasitology 75: 519-523.

Platt, T.R., and W.M. Samuel. 1984. Mode of entry of first-stage larvae of *Parelaphostrongylus odocoilei* (Nematoda: Metastrongyloidea) into four species of terrestrial gastropods. Proceedings of the Helminthological Society of Washington 51: 205-207.

Prestwood, A.K., and J.F. Smith. 1969. Distribution of meningeal worm (*Pneumostrongylus tenuis*) in deer in the southeastern United States. The Journal of Parasitology 55: 720-725.

Pursglove, S.R. 1977. Helminth parasites of white-tailed deer (*Odocoileus virginianus*) from New Jersey and Oklahoma. Proceedings of the Helminthological Society of Washington 44: 107-108.

Pybus, M.J., W.M. Samuel, D.A. Welch, J. Smits, and J.C. Haigh. 1992. Mortality of fallow deer (*Dama dama*) experimentally-infected with meningeal worm, *Parelaphostrongylus tenuis*.

Rogers, L.L. 1987. Seasonal changes in defecation rates of free-ranging white-tailed deer. The Journal of Wildlife Management. 51: 330-333.

Rowley, M.A., E.S. Loker, J.F. Pagels, and R.J. Montali. 1987. Terrestrial gastropod hosts of *Parelaphostrongylus tenuis* at the National Zoological Park's Conservation and Research Center, Virginia. The Journal of Parasitology 73: 1084-1089.

Samuel, W.M. 1969. Parasites of the white-tailed deer in south Texas. Ph.D. Thesis, University of Wisconsin, Madison. 196pp.

Samuel, W.M. 1987. Moving the zoo or the potential introduction of a dangerous parasite into Alberta with its translocated host. In: Renecker, L.A.(ed.) Focus on a New Industry. Proceedings of the Alberta Game Growers' Association Conference 1: 85-92

Samuel, W.M. 1991. A partially annotated bibliography of meningeal worm, Parelaphostrongylus tenuis (Nematoda), and its close relatives. In: M.J. Kennedy (ed.). Synopsis of the Parasites of Vertebrates. Alberta Agriculture, Animal Health Division, Queen's Printer, Edmonton, AB, 36 pp.

Samuel, W.M., and R.L. Beaudoin. 1966. Evaluation of two survey methods for detection of helminth infections in white-tailed deer (*Odocoileus virginianus*). Wildlife Disease Association Bulletin 2: 100-107.

Samuel, W.M., and D.O. Trainer. 1969. A technique for survey of some helminth and protozoan infections of white-tailed deer. The Journal of Wildlife Management 33: 888-894.

Samuel, W.M., and J.C. Holmes. 1974. Search for elaphostrongyline parasites in cervids from Alberta. Canadian Journal of Zoology 52: 401-403.

Samuel, W.M., T.R. Platt, and S.M. Knispel-Krause. 1984. Gastropod intermediate hosts and transmission of *Parelaphostrongylus odocoilei*, a muscle-inhabiting nematode of mule deer, *Odocoileus hemionus*, in Jasper National Park, Alberta. Canadian Journal of Zoology 63: 928-932.

Samuel, W.M., M.J. Pybus, D.A. Welch, and C.J. Wilke. 1992. Elk as a potential host for meningeal worm: Implications for translocation. Journal of Wildlife Management 56: 629-639.

SAS Institute Inc. 1989. JMP users guide., Cary, NC, USA. pp. 305-316

Senger, C.M. 1964. Lethal effect of ultraviolet radiation on free-living nematodirid larvae. The Journal of Parasitology. 50: 56.

Severinghaus, C.W. 1949. Tooth development as criteria of age in white-tailed deer. Journal of Wildlife Management 13: 195-216

Shoesmith, M.W. 1976. Mule Deer. The true jumpers of Manitoba. Department of Natural Resources, Information Series Number 13. 15pp.

Shostak, A.W., and W.M. Samuel. 1984. Moisture and temperature effects of survival and infectivity of first-stage larvae of *Parelaphostrongylus odocoilei* and *P. tenuis* (Nematoda: Metastrongyloidea). The Journal of Parasitology 70: 261-269.

Slomke, A.M., M.W. Lankester, and W.J. Peterson. 1995. Infrapopulation Dynamics of *Parelaphostrongylus tenuis* in white-tailed deer. Journal of Wildlife Disease. 31(2): 125-135

Smith, H.J., R.M. Archibald, and A.H. Corner. 1964. Elaphostrongylosis in maritime moose and deer. Canadian Veterinary Journal 5: 287-296.

Sokal, R.R. and F.J. Rohlf. 1980. Biometry: The Principles and Practices of Statistics in Biological Research. W. H. Freeman and Company. San Francisco, California, USA.

Sparrowe, R.D., and P.F. Springer. 1970. Seasonal activity patterns of white-tailed deer in eastern South Dakota. The Journal of Wildlife Management 34: 420-431.

Stoutjesdijk, P. and J.J. Barkman. 1992. *In* Microclimate Vegetation and Fauna. Opulus Press AB. Knivsta. Sweden.

Thomas, J.E., and D.G. Dodds. 1988. Brainworm, *Parelaphostrongylus tenuis*, in moose, *Alces alces*, and white-tailed Deer, *Odocoileus virginianus*, of Nova Scotia. Canadian Field-Naturalist 102: 639-642.

Thurston, D.R., and R.G. Strout. 1978. Prevalence of meningeal worm (*Parelaphostrongylus tenuis*) in white-tailed deer from New Hampshire. Journal of Wildlife Diseases 14: 89-96.

Upshall, S.M., M.D.B. Burt. and T.G. Dilworth. 1987. *Parelaphostrongylus tenuis* in New Brunswick: the parasite in white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*). Journal of Wildlife Diseases 23: 683-685.

Van Es, J., and D.A. Boag. 1981 Terrestrial molluscs of central Alberta. Canadian Field-naturalist 95: 75-99.

Watson, T. G. 1984. Tissue worm in red deer. Symptoms and control. AgLink FPP249, Media Services, Min. Agr. and Food Wellington, New Zealand.

Whitlock, J.H. 1952. Neurofilariosis, a paralytic disease of sheep: II. *Neurofilaria cornellensis*, n.g., n.sp. (Nematoda, Filarioidea), a new nematode parasite from the spinal cord of sheep. Cornell Veterinarian 42: 125-132.

Whitlock, J.H. 1959. *Elaphostrongylus*, the proper designation of *Neurofilaria*. Cornell Veterinarian 49: 3-14.

Watson, T. G. 1984. Tissue worm in red deer. Symptoms and control. AgLink FPP249, Media Services, Min. Agr. and Food Wellington, New Zealand.

Zar, J.H. 1984. Biostatistical Analysis. Second Edition. Prentice Hall, Englewood Cliffs, New Jersey USA.

Appendix IA. Climate stations for selected Gun Hunting Areas in Manitoba.

Wildlife Management Unit	Station Name
A05	FLIN FLON A
A06	THE PAS A
A06A	THE PAS A
A12	OVERFLOWING R.
A13	BIRCH RIVER
A14	BIRCH RIVER
A15	BIRCH RIVER
A18	SWAN RIVER
A18A	SWAN RIVER
A19	DAUPHIN A
A19A	WINNEPEGOSIS SE
A19B	DAUPHIN A
A20	GYPSUMVILLE
A21	MOOSEHORN COOK
A22	HAMIOTA
A23	WASAGAMING
A23A	DAUPHIN A
A24	NEEPAWA WATER
A25	VOGAR
A25A	ARBORG
A25B	STONEWALL
A26	BISSETT
A27	RESTON
A28	SOURIS
A29	Boissevain 2
A29A	Boissevain 2
A30	BRANDON A
A31	MORDEN CDA
A31A	PILOT MOUND 2 (PO)
A32	PORTAGE LA PRAIRIE A
A33	ALTONA
A34	PINAWA WNRE
A34A	WINNEPEG INTL
A35	SPRAGUE
A35A	NIVERVILLE
A35A1	STEINBACH
A36	RENNIE
A38	WINNEPEG STP

Appendix IB. Climate stations for selected Gun Hunting Units in North Dakota.

Wildlife Management Unit	Station Name
U2A	WAHPETON 3 N
U2B	HILLSBORO 3N
U2C	GRAFTON
U2D	CAVALIER 7 NW
U2E	EDMORE 1 N
U2F1	MC HENRY
U2F2	EDMUNDS ARROWWOOD REF
U2G	JAMESTOWN FAA AIRPORT
U2G1	MC LEOD 3 E
U2G2	FORMAN 5 SSE
U2H	ASHLEY
U2I	NAPOLEON
U2J1	BISMARCK WSFO AP
U2J2	PETTIBONE
U2K1	BUTTE
U2K2	RUGBY
U2L	DEVILS LAKE KDLR
U3A1	WILDROSE
U3A2	MOHALL
U3A3	GARRISON 1NNW
U3A4	UPHAM 3N
U3B1	WILLISTON WSO
U3B3	WASHBURN
U3C	FT. YATES
U3D2	CENTER 4 SE
U3E1	DICKINSON FAA AP
U3E2	NEW SALEM
U3F1	HETTINGER
U4B	WATFORD CITY 14 S
U4D	BEACH
U4F	BOWMAN CRT HSE

Appendix IC. Climate stations for selected Wildlife Management Zones in Saskatchewan.

Wildlife Management Unit	Station Name
Z03	CLAYDON
Z05	SWIFT CURRENT CDA
Z06	MAPLE CK N
Z07	MAPLE CK N
Z08	GOLDEN PRAIRIE
Z09	TOMPKINS
Z11	LEADER 2
Z12	ABBEY
Z15	ESTEVAN A
Z16	WEYBURN
Z17	MONTMARTE
Z18	DAHINDA
Z19	PARKBEG
Z20	MOOSE JAW A
Z22	WATROUS
Z24	DINSMORE
Z25	BICKLEIGH
Z26	BICKLEIGH
Z28	HARRIS
Z29	HARRIS
Z31	OXBOW
Z32	REDVERS
Z33	CARLYLE
Z34	MOOSOMIN
Z35	ROCANVILLE SYLVITE
Z36	INDIAN HEAD PFRA
Z37	LANGENBURG
Z38	WISHART
Z39	FOAM LAKE
Z40	KUROKI
Z41	HUMBOLDT
Z42	MELFORT CDA
Z43	NIPAWIN A
Z44	NORTH BATTLEFORD A
Z45	CANDO
Z46	UNITY SOUTH
Z47	NORTH BATTLEFORD A
Z48	PREECEVILLE
Z49	HUDSON BAY A
Z50	CHOICELAND
Z51	PRINCE ALBERT A
Z52	PRINCE ALBERT A
Z53	PRINCE ALBERT A
Z54	NORTH BATTLEFORD A
Z55	MEADOW LAKE A
Z56	ENDEAVOUR
Z57	HUDSON BAY A
Z58	HUDSON BAY A
Z59	HUDSON BAY A
Z60	FLIN FLON A
Z61	FLIN FLON A

Appendix IIA. Significance level for t-test comparing means of all ecological variables between deer management units with *Parelaphostrongylus tenuis* present and deer management units with *P. tenuis* absent for all units sampled in Manitoba and Saskatchewan.

Ecological Variable	P Value
January DMAXT	0.167
February DMAXT	0.025
March DMAXT	0.604
April DMAXT	0.093
May DMAXT	0.044
June DMAXT	0.419
July DMAXT	0.36
August DMAXT	0.21
September DMAXT	0.244
October DMAXT	0.921
November DMAXT	0.419
December DMAXT	0.055
YEAR DMAXT	0.146
January DMINT	0.037
February DMINT	0.006
March DMINT	0.088
April DMINT	0.111
May DMINT	0.28
June DMINT	0.402
July DMINT	0.165
August DMINT	0.182
September DMINT	0.064
October DMINT	0.005
November DMINT	0.213
December DMINT	0.04
YEAR DMINT	0.385
January DMEANT	0.046
February DMEANT	0.007

March DMEANT	0.162
April DMEANT	0.102
May DMEANT	0.092
June DMEANT	0.641
July DMEANT	0.692
August DMEANT	0.962
September DMEANT	0.801
October DMEANT	0.624
November DMEANT	0.91
December DMEANT	0.046
YEAR DMEANT	0.237
January MEANSNOW (cm)	0.006
February MEANSNOW (cm)	0.101
March MEANSNOW (cm)	0.002
April MEANSNOW (cm)	0.097
May MEANSNOW (cm)	0.087
June MEANSNOW (cm)	0.271
July MEANSNOW (cm)	na
August MEANSNOW (cm)	na
September MEANSNOW (cm)	< 0.001
October MEANSNOW (cm)	0.807
November MEANSNOW (cm)	< 0.001
December MEANSNOW (cm)	0.12
YEAR MEANSNOW (cm)	0.006
January MEANRAIN (mm)	0.177
February MEANRAIN (mm)	0.218
March MEANRAIN (mm)	0.004
April MEANRAIN (mm)	0.041
May MEANRAIN (mm)	0.152
June MEANRAIN (mm)	0.04
July MEANRAIN (mm)	0.061
August MEANRAIN (mm)	< 0.001

September MEANRAIN (mm)	< 0.001
October MEANRAIN (mm)	< 0.001
November MEANRAIN (mm)	0.002
December MEANRAIN (mm)	0.514
YEAR MEANRAIN (mm)	< 0.001
January MEAN PRECIP (mm)	0.005
February MEAN PRECIP (mm)	0.053
March MEAN PRECIP (mm)	0.007
April MEAN PRECIP (mm)	0.005
May MEAN PRECIP (mm)	0.097
June MEAN PRECIP (mm)	0.039
July MEAN PRECIP (mm)	0.056
August MEAN PRECIP (mm)	< 0.001
September MEAN PRECIP (mm)	< 0.001
October MEAN PRECIP (mm)	< 0.001
November MEAN PRECIP (mm)	< 0.001
December MEAN PRECIP (mm)	0.043
YEAR MEAN PRECIP (mm)	< 0.001
January DAYSRAIN	na
February DAYSRAIN	0.58
March DAYSRAIN	0.136
April DAYSRAIN	0.351
May DAYSRAIN	0.143
June DAYSRAIN	0.257
July DAYSRAIN	0.017
August DAYSRAIN	0.006
September DAYSRAIN	0.002
October DAYSRAIN	< 0.001
November DAYSRAIN	0.001
December DAYSRAIN	0.431
YEAR DAYSRAIN	0.003

January DAYSPRECIP	0.32
February DAYSPRECIP	0.393
March DAYSPRECIP	0.07
April DAYSPRECIP	0.076
May DAYSPRECIP	0.009
June DAYSPRECIP	0.261
July DAYSPRECIP	0.022
August DAYSPRECIP	0.003
September DAYSPRECIP	0.003
October DAYSPRECIP	< 0.001
November DAYSPRECIP	0.014
December DAYSPRECIP	0.122
YEAR DAYSPRECIP	0.02
Latitude	0.45
Longitude	< 0.001
Elevation	< 0.001
Winter (DJF) TEMP	0.025
Spring (MAM) TEMP	0.114
Summer (JJA) TEMP	0.794
Fall (SON) TEMP	0.847
Winter (DJF) MPRECIP	0.004
Spring (MAM) MPRECIP	0.006
Summer (JJA) MPRECIP	< 0.001
Fall (SON) MPRECIP	< 0.001

Appendix IIB. Significance level for t-test comparing means of all ecological variables between deer management units with *Parelaphostrongylus tenuis* present and deer management units with *P. tenuis* absent for all units sampled in North Dakota.

Climate Variable	P value - Annual	P Value - Normals
Normal Annual Precipitation	NA	0.005
Normal Annual Temperature	NA	0.14
January Total Precipitation	0.011	< 0.001
February Total Precipitation	0.003	0.841
March Total Precipitation	0.021	< 0.001
April Total Precipitation	0.021	< 0.001
May Total Precipitation	0.007	0.542
June Total Precipitation	0.767	0.876
July Total Precipitation	0.237	0.01
August Total Precipitation	0.011	< 0.001
September Total Precipitation	0.13	0.002
October Total Precipitation	0.855	< 0.001
November Total Precipitation	0.591	0.02
December Total Precipitation	0.361	0.042
January Mean Temp	0.026	0.0217
February Mean Temp	0.085	0.0254
March Mean Temp	0.012	0.1343
April Mean Temp	0.294	0.8009
May Mean Temp	0.414	0.063
June Mean Temp	0.501	0.0973
July Mean Temp	0.497	0.8547
August Mean Temp	0.069	0.5491
September Mean Temp	0.143	0.5288
October Mean Temp	0.867	0.6147
November Mean Temp	0.1	0.2404
December Mean Temp	0.146	0.0124

Appendix III. Month of death for all white-tailed deer collected.

Number of deer	Year	State/Province	% Killed in November
238	1989	ND	99
300	1990	ND	99
592	1989	MB	92
171	1990	MB	94
90	1989	SK	92
475	1990	SK	89

Appendix IV) Epidemiology of *Parelaphostrongylus tenuis*

The epidemiology (movement and establishment) of *P. tenuis* likely occurs in the following chronological sequence.

1) Patent white-tailed deer move into a "new area" (no *P. tenuis* present).

2) Once immigrating deer establish home ranges, they adapt to their daily routines of moving to and from bedding areas and feeding areas, defecating as they travel (mean daily defecation = 12 pellet groups x 225 g/ pellet group = 3600 g (Rogers 1987).

3) The longer an infected deer lives, and the longer it remains in a localized area, the more abundant first stage larvae become in the environment.

4) Higher densities of patent deer further increase the probability that more deer will become infected. More patent deer in the environment will result in an increase in the number of first stage larvae in the environment.

5) If a threshold amount of feces is deposited in an area with suitable gastropod intermediate hosts, and if the first stage larvae survive long enough (*i.e.*, dependent on desiccation, thaw-freezing cycles, and washing away from fecal pellets into a poor site) to be encountered by a suitable intermediate host, then prevalence of infected gastropods will increase.

6) Density of suitable intermediate hosts is highly dependent on climatic conditions. In dry hot summers, numbers may decrease and in moist warm summers high survivorship may result in high densities of gastropods. Intermediate hosts must become infective, remain active, and occur in great enough densities, for a long enough period in deer summer feeding areas to increase their likelihood of being accidentally ingested by a white-tailed deer.

7) Deer must feed close to the ground in suitable gastropod habitat to increase the likelihood of uninfected deer becoming infected and passing viable first stage larvae

8) Once deer have ingested viable third stage larvae they must live long enough (*i.e.*, avoid predation, hunter harvest, vehicular collision) to become patent.

If all the previous conditions are met, and the odds are high enough, it is probable that *P. tenuis* will become established. On the edge of the known eastward distribution of *P. tenuis*, critical ecological factors such as temperature, precipitation, deer density, and gastropod habitat are likely near threshold values. Annual fluctuations of these ecological parameters, and the time-lag effect these parameters may have on determining whether or not *P. tenuis* can be successfully transmitted results in a "gray zone" or undefined distributional boundary. The range limit of *P. tenuis* would be in a continual state of flux, advancing westward and northward following successive years of favorable conditions and receding during successive years of unfavorable conditions.