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MOVEMENTS, RESOURCE SELECTION, AND RISK ANALYSES FOR PARASITIC DISEASE IN AN EXPANDING MOOSE POPULATION IN THE NORTHERN GREAT PLAINS

by

James J. Maskey Jr.
Bachelor of Science, Northern Michigan University, 1999
Master of Science, Northern Michigan University, 2002

A Dissertation
Submitted to the Graduate Faculty
of the
University of North Dakota
in partial fulfillment of the requirements

for the degree of
Doctor of Philosophy

Grand Forks, North Dakota
December
2008
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Department: Biology
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ABSTRACT

Little is known regarding moose ecology in North Dakota, and a decline in moose in northeastern North Dakota may be linked to parasites of white-tailed deer (*Parelaphostrongylus tenuis* and *Fascioloides magna*). I investigated the ecology of moose, including the potential effects of parasitic disease. I used global positioning system collars to estimate home ranges and habitat selection and collected fecal samples for diet estimates. I reviewed historical data and examined livers moose for evidence of *F. magna* infection. I examined 3730 white-tailed deer for *P. tenuis* and investigated whether prevalence had increased since 1991. I modeled the relationship of climate, habitat and deer density to *P. tenuis* prevalence and sampled gastropod intermediate hosts to determine habitats functioning in *P. tenuis* transmission. I estimated moose harvest rates, investigated climate trends, and compared moose population trends to climate for three areas. Finally, I created a risk map for *P. tenuis* infection that incorporated climate, deer density and habitat.

Home ranges ($F_1 = 30.9, P < 0.001$) and habitat use ($F_1 = 30.9, P < 0.001$) differed between study sites. Moose selected for wooded habitats, and primarily consumed woody browse ($> 65\%$). Habitat spatial pattern likely influenced home range size, and moose range expansion to the prairie appears related to human-induced habitat change. Historical data revealed that *F. magna* is endemic to North Dakota, although this parasite was absent in moose livers collected from 2002-2003. This parasite is probably not a primary factor in moose declines, and a lack of permanent wetlands may limit
transmission. *P. tenuis* prevalence in deer was 14%, and had increased since 1991 (P = 0.05). A model of growing season precipitation, winter temperature, and growing season temperature best predicted prevalence ($r^2 = 0.84$). Gastropod sampling suggested that woodlands are critical to *P. tenuis* transmission. Harvest rates ranged from 16.8-26.7%. Summer temperatures were cooler; May-June precipitation increased, and growing season lengthened. In northeastern North Dakota, *P. tenuis* risk was higher, and population trends were correlated with climate. Moose declines are likely due to overexploitation and increasing *P. tenuis* transmission resulting from a wetter climate and increased deer abundance.
Background and Introduction

Historically, and into the present, moose have been an important species for native North Americans both as a source of subsistence and for cultural reasons (Reeves and McCabe 1998). Moose are also a prized game species, and as non-consumptive uses of wildlife have become more popular, the species is equally important for its aesthetic qualities (Crichton et al. 1998). Management and conservation of moose requires an understanding of all aspects of its biology and its relationship to the environment. This includes habitat needs, relationships with predators and pathogens, and the impacts that humans can have on these processes. The challenge for current management of moose populations is to balance scientific management with the needs of humans in the face of changing ecosystems and changing public attitudes about wildlife (Crichton et al. 1998).

Distribution and Relevant Taxonomy

Moose (*Alces alces*) are the largest extant member of the deer family (Cervidae) with adult males of the species weighing up to 710 kg (Bubenik 1998). Moose have a circumboreal distribution and occur widely across the northern parts of North America and Eurasia in association with boreal forest. Moose are unique in that they have no counterpart in the southern hemisphere (Shelford 1963). The distribution of moose is limited by food and lack of cover to the north and by warm climate to the south.
(Renecker and Hudson 1986, Kelsall and Telfer 1974). Four subspecies of moose are recognized in North America (Bubenik 1998). The Shiras or Yellowstone moose (Alces alces shirasi) is the smallest of the subspecies with bulls weighing 370 kg or less. Shiras moose occur in western Wyoming, eastern and northern Idaho, western Montana, southern Alberta, southeastern British Columbia, northeastern Utah, and Colorado. The eastern or taiga moose (A. a americana) is a larger form, weighing up to 600 kg, found in Maine, Nova Scotia, Quebec, eastern Ontario, and Newfoundland. The northwestern moose (A. a. andersoni) is about the same size as A. a. americana and is found northern Michigan, Minnesota, North Dakota, Western Ontario, Manitoba, central British Columbia, the eastern Yukon, and the Northwest Territories. The Alaska/Yukon or tundra moose (A. a. gigas) is the largest of the North American subspecies, with bulls weighing as much as 710 kg. The tundra moose occurs across northern British Columbia and the Yukon Territory, Canada, and in the state of Alaska, (Bubenik 1998).

Social and Reproductive Behaviors

Moose are chiefly solitary animals with bulls and yearlings spending most of the year alone and cows associating primarily with their calves. Bull and cow moose are found together during the approximate one month breeding season starting around early October. (Baker 1983). Moose are not territorial in that they are not agonistic to each other, and their home ranges overlap (Phillips et al. 1973). Cows typically give greater space to cows with calves than to single cows, however, and Cederlund et al. (1987) described moose as having a "sliding territory" around them. The mating season typically begins in September or October with a period of searching and calling by both male and female moose. This is followed by a short courtship period, a driving or
following stage, and finally, by mating (Baker 1983, Markgren 1974). Moose are thought to be conditionally polygamous. Because the courtship period extends over several days and females are receptive for only a short period, bulls likely do not have time to find more than one mate except in areas of high population density (Markgren 1974). Following a gestation period of 240-246 days, one or two calves are born in late May or early June (Baker 1983). Calves typically stay with their mother until the following May or June.

Diet

Moose are predominately browsers with forbs, grasses, and sedges generally playing a minor role in their diets. Moose generally consume the leaves of browse species in summer and the twigs in winter (Renecker and Schwartz 1998). Several species of trees/shrubs favored by moose for browse include balsam fir (Abies balsamea), aspen (Populus spp.), paper birch (Betula papyrifera), willow (Salix spp.) red osier dogwood (Cornus stolonifera), maple (Acer spp.), mountain ash (Sorbus Americana) and beaked hazel (Corylus cornuta) (Jones and Hobson 1985, Belovsky 1981). Moose consume aquatic plants such as eelgrass (Vallisneria Americana), pondweed (Potamogeton spp.), yellow water lily (Nuphar advena), and bulrush (Scirpus spp.) (Jones and Hobson 1985, De Vos 1958) and green algae such as chara and Spirogyra, the latter of which they drink in with water in areas where it occurs in dense concentrations (Belovsky and Jordan 1981). Researchers have speculated that aquatic vegetation is a critical source of sodium for moose, especially in environments where sodium from other sources is in short supply (Belovsky and Jordan 1981).
Habitat Use /Habitat Requirements

Moose occupy both stable and transitory habitats (Geist 1971). Transitory habitats are those subject to disturbance or successional processes. In the boreal forest habitats that moose are typically associated with, moose prefer the early-successional stages that were historically created by fire and spruce budworm (Peek et al. 1976, Peterson 1955). In areas where fire was historically important, logging may now fulfill the same function. Moose are known to utilize areas of forest that were clear-cut logged, and moose numbers in logged areas have been reported to increase when hunting pressure is not overly heavy (Rempel et al. 1997, Leptich and Gibert 1989). Moose also occupy more stable habitats that persist through time, such as river delta systems where annual flooding maintains willow habitat. Other such stable habitat types used by moose include scrub/ shrub habitats, mesic maritime forest, and montane forests. Moose will also use aquatic habitats in the spring and summer to obtain dietary minerals, to cool themselves, and to avoid insects (Belovsky and Jordan 1981, Peek 1998, Peek et al. 1976). The distribution of moose is primarily related to availability of adequate forage of different types throughout the year, though in severe winter conditions moose may use mature conifer habitats to escape deep snows (Kelsall 1969). Evidence suggests that foraging by moose can affect habitats through altering of the nutrient cycle and inhibition or the regeneration of preferred browse species (Pastor et al. 1993, Maclnnes et al. 1992).

Home Range / Movements

Moose home range sizes are considerably variable, ranging from as small as 2km² up to 92km² (Cederlund and Sand 1994, Ballard et al. 1991, Leptich and Gilbert 1989, Grauvogel 1984). Moose may migrate between seasonal home ranges or remain in
the same area year round subject to behavioral and energetic constraints (Hundertmark 1998). Home ranges of cows are smaller at the time of calving (Cederlund et al. 1987), though range size overall does not appear to differ seasonally (Ballard et al. 1991).

Seasonal migrations vary in distance from 2 to 170 km and may have a traditional pattern (Anderson 1991, LeResche 1974, Berg 1971, Barry 1961). Dispersal from natal range is usually of short distance, although longer distance dispersal events have been observed (Mytton and Keith 1981). Cederlund et al. (1987) found that dispersal of calves from their native range was shorter in areas with abundant forage resources. Ballard et al. (1991) reported that dispersal is greater in areas where moose densities are high, while Labonte et al. (1998) determined that lightly harvested areas may contribute to the moose harvest in heavily harvested areas and that these refuges may contribute to the population in surrounding areas.

Population Trends and Status

Moose populations are subject to fluctuation of processes that affect both limiting and regulating factors. Reported moose densities vary widely from as low as 0.148 moose/km² in parts of Alaska with abundant predators (Gasaway et al. 1992) to 2.25 moose/km² in Quebec (Crete 1987). The absolute number of moose in North America has increased since the mid 20th Century, although Franzmann (2000) considered that moose populations in 1990 were not significantly larger than they were in 1960. Nonetheless, during this period moose range and numbers have increased in many areas of North America as a result of natural range expansion and translocations (Boer 1992, Knue 1991, Aho and Hendrickson 1989), although there is recent evidence of moose declines in some areas Murray et al. (2006).
Important Mortality Factors

Where predators are present, a large proportion of the annual mortality in many moose populations occurs among neonates less than 6 months old (Bertram and Vivion 2002, Van Ballenberghe and Ballard 1998). For example, black and grizzly bears can kill upwards of 50% of newborn moose (Ballard 1992), while wolves may take greater than 18% of moose calves (Gasaway et al. 1983). Predators can also cause significant mortality in adult moose. Boertje et al. (1988) reported that grizzly bears killed between 0.6 to 3.9 adult moose/year. Wolves may also reduce the annual survival of adult moose. Wolves generally take older-aged moose independent of body condition, and in areas where moose are their primary prey, wolves may kill one adult moose every 7-16 days (Bertram and Vivion 2002, Ballard et al. 1987, Peterson et al. 1984, James 1983). Deep snow conditions can increase the vulnerability of moose to predation by wolves (Mech et al. 1987). Removal of wolves has been shown to increase moose populations through improved adult survival, and to a lesser degree, through increased recruitment (Hayes et al. 2003). Recently, Post et al. (2002) provided evidence that moose and wolf populations were in phase-dependent multi-annual cyclic fluctuations on Isle Royale. In this case, moose populations were regulated by wolves during periods of wolf increase and moose decline, while moose exhibited stronger self-regulation during periods of wolf decrease and moose increase. This represented the first documentation of population cycles in large mammals.

Disease may also serve as an important mortality factor for moose. Transmission of two important parasitic diseases of moose, meningeal worm (*Parelaphostrongylus tenuis*) and liver fluke (*Fascioloides magna*) may have increased by recent range...
expansion and population increases of white-tailed deer (*Odocoileus virginianus*). Meningeal worm is a nematode parasite that occurs in the dura mater, subdural space and venous sinuses of the cranium of its normal definitive host, the white-tailed deer (Anderson and Prestwood 1981). Deer become infected when they ingest a gastropod infected with third-stage larvae of *P. tenuis*. Once in the alimentary canal, the larvae exit the gastropod, penetrate the gastrointestinal wall, and cross the peritoneal cavity (Anderson and Prestwood 1981). Worms then migrate to the cranium where they mate and deposit eggs in the veins. Eggs travel to the lungs where they hatch into first-stage larvae. These larvae traverse the bronchial tree, are swallowed by the host and are passed out with the feces (Anderson and Prestwood 1981, Samuel et al. 1992; Figure 1).

Prevalence of infection in white-tailed deer is often greater than 50% (Anderson and Prestwood 1981). In moose *P. tenuis* is unable to complete its life cycle and neurological disease is the result of high parasite activity in host neural tissue and damage to brain tissue when worms coil upon themselves or enter and invade the neural parenchyma and/or ependymal canal. Signs of neurological disease in moose include loss of fear, blindness, holding head to one side, walking aimlessly or in circles, and partial paralysis (Olson and Woolf 1978). *P. tenuis* requires a terrestrial gastropod to serve as an intermediate host, and at least 26 species of snails and slugs may function in this role (Lankester 2001; Figure 1). Infected gastropods are commonly found in low damp forested areas (Lankester and Anderson 1968).

Declines in moose populations have been attributed to *P. tenuis*, and the size of moose populations has been shown to be negatively correlated to *P. tenuis* prevalence in deer (Gilbert 1973, Karns 1967) as well as deer density and larval shedding intensity.
(Anderson and Prestwood 1981). Whether *P. tenuis* is the cause of these population decreases has been the subject of much debate (Gilbert 1992, Nudds 1990, Nudds 1992). Whitlaw and Lankester (1994) and Dumont and Crete (1996) revisited this question, however, and concluded that *P. tenuis* may be a limiting factor for some moose populations.

Adult *F. magna* occur in pairs or groups within fibrous capsules in the liver parenchyma of definitive hosts such as white-tailed deer. Definitive hosts become infected by eating vegetation containing fluke cysts. Larval *F. magna* exit the small intestine and move to the host’s liver where they migrate through the liver tissue until they become encapsulated (Foreyt et al. 1977, Foreyt and Todd 1976; Figure 2). White-tailed deer are a normal host for *F. magna*. Infection in white-tailed deer can result in significant liver damage as a result of tissue destruction by migrating larvae and encapsulated adults, but unless they are heavily infected by *F. magna*, most individual deer survive in relatively good condition with few clinical signs of infection (Huot 1989, Torbit et al. 1985, Reimers et al. 1982, Pursglove et al. 1977). In dead-end hosts such as moose, however, juvenile flukes migrate much more extensively before becoming encapsulated, which can cause extensive damage or fibrosis to 50-90% of the animal’s liver tissue, often leading to death (Pybus 2001, Aho and Hendrickson 1989, Lankester 1974, Karns 1972). In dead-end hosts, the capsules enveloping adult flukes are much thicker walled than those found in normal hosts and prevent the escape of eggs and the completion of the fluke life-cycle (Pybus 2001). A long-term decline in moose numbers in northwestern Minnesota has recently been linked to infection by liver flukes (Murray
**P. tenuis Life Cycle**

![Diagram showing the life cycle of Parelaphostrongylus tenuis]

- Infected snails ingested
- 1st stage larvae shed in feces
- Larvae develop to 3rd stage
- 1st stage larvae penetrate intermediate host

Figure 1. Life cycle of the meningeal worm (*Parelaphostrongylus tenuis*).

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**F. Magna Life Cycle**

![Diagram showing the life cycle of Fascioloides magna]

- Deer ingest aquatic veg containing cysts
- Miracidia enter aquatic snails
- Cercaria encyst on emergent vegetation

Figure 2. Life cycle of the liver fluke (*Fascioloides magna*).
et al. 2006). Other sources of mortality that may be important for moose are winter tick infestations (observed (Glines and Samuel 1989, Addison and Smith 1981), overharvest and poaching (Timmermann and Buss 1998), and moose-car and moose-train collisions (Child 1998). These latter sources of mortality increase as human activity encroaches on moose habitat (Oosenberg et al. 1991).

History of Moose in North Dakota

The historic distribution of moose (*Alces alces*) in North Dakota included the more forested habitats of the Turtle Mountains and Pembina Hills areas (Knue 1991). By the late 1880s moose were all but extirpated from the state, and for several decades there was not much hope for the return of moose to North Dakota. However, by the 1950s occasional sightings of moose in North Dakota were reported, and by the late 1960s a resident population of moose had become established in the Pembina Hills. Moose also were seen during this time along the Canadian border and Red River (Knue 1991). In addition to re-colonizing the traditional habitats they previously occupied in North Dakota, moose began to expand their range to include the prairie coteau region of the state. Expansion of moose in the prairie coteau has been attributed to changes in the landscape that provided moose with planted woodlands as a source of food and cover as well as the end of subsistence hunting by area residents (Johnson 1991). The state of North Dakota held its first hunting season for moose in 1977. Ten permits for bull moose were issued, and nine of the ten hunters were successful (Knue 1991). Since that time, the number and range of moose in North Dakota has continued to increase. Currently, around 150 hunting licenses for moose are issued annually, and the moose population in
the state is estimated at 500-1000 animals (Johnson 2002, W. F Jensen, Big Game
Biologist North Dakota Game and Fish Department, pers. comm. 2002).

Background and Purpose of this Study

Although multiple studies have examined moose movements and habitat use in
woodland habitats (Labonte et al. 1998, MacCracken et al. 1997, Cederlund and Sand
1994, Leptich and Gilbert 1989, Kearney and Gilbert 1976), research on moose in prairie
ecosystems is lacking, and moose research in North Dakota has not previously been
conducted. Thus, very little is known regarding seasonal movements, habitat use, and
basic population ecology of moose (Alces alces) in prairie habitats in North Dakota. In
addition, the recent expansion by moose into the prairie coteau of central North Dakota
where the population of white-tailed deer is recently burgeoning (Smith et al. 2007)
creates the potential for overlap in habitat use between these two Cervids. Overlap in
habitat use between moose and white-tailed deer may have significant negative
consequences for moose by the spread of P. tenuis and F. magna into moose populations
Murray et al. 2001). Recent reports of moose in North Dakota exhibiting signs of
infection by P. tenuis (North Dakota Game and Fish Department, unpublished data), and
documentation that F. magna was the primary factor causing a long-term decline in
moose numbers in an adjacent area of northwestern Minnesota (Murray et al. 2006) has
only heightened these concerns. Thus the purpose of this project was to investigate the
overall ecology of moose in North Dakota, including identifying important sources of
mortality and the role disease may play in moose population dynamics.
This dissertation is organized into four main chapters that each address specific objectives related to the purpose of this project. Chapter II focuses on my investigation of the movements, habitats use and diets of North Dakota moose in their traditional habitats in the Turtle Mountains and in more recently colonized habitats of the prairie. Chapter III covers my examination of the occurrence of *F. magna* in North Dakota moose, its transmission potential in the state, and its possible role as a mortality factor for moose. The prevalence, geographic range and transmission potential of *P. tenuis* in white-tailed deer in North Dakota is the focus of chapter IV, while Chapter V focuses on the role of hunter harvest, climate, deer density, and disease in influencing moose population trends in North Dakota.
CHAPTER II

MOVEMENTS AND RESOURCE USE BY RECOLONIZING MOOSE IN TRADITIONAL AND NONTRADITIONAL HABITATS IN NORTH DAKOTA

Introduction

Moose are the largest extant members of the deer family and enjoy a circumboreal distribution, which includes much of the northern portion of North America. Throughout their range, moose occupy both stable and those created by periodic disturbance. Moose distribution and habitat use is primarily related to the availability of forage throughout the year. However, moose may also select habitats that provide thermal cover or aid in predator avoidance (Dussault et al. 2005, Kelsall 1969). Accordingly, annual home range sizes are considerably variable, ranging from as small as 2 km$^2$ up to 92 km$^2$ (Cederlund and Sand 1994, Ballard et al. 1991, Leptich and Gilbert 1989, Grauvogel 1984), and moose may migrate between seasonal home ranges or remain in the same area year round subject to behavioral and energetic constraints (Hundertmark 1998).

Moose are native to North Dakota with their traditional range encompassing the aspen (*Populus tremuloides*) and bur oak (*Quercus macrocarpa*) forests of the Turtle Mountains and Pembina Hills along the northern edge of the state (Knue 1991). While moose were extirpated from North Dakota by the late 1800s, they had begun to re-establish a population in the state by the 1960s. In addition to re-colonizing their
historic range, moose were also observed in new areas and non-traditional "prairie" habitats in North Dakota after the 1970s. By the 1980s, moose had expanded their range to include large expanses of former tall and mixed grass prairie that had been greatly modified by conversion to agriculture and widespread planting of tree rows/shelter belts to reduce wind erosion subsequent to the Dust Bowl years of the 1930s (Knue 1991, Licht 1997).

The colonization and expansion by moose into the Lake Agassiz and Northern Glaciated Plains ecoregions of North Dakota (Figure 8) is likely the result of conversion of the native prairie landscape to an agricultural mosaic that provides moose with suitable cover and forage otherwise absent in unaltered tall of mixed grass prairie habitats. Although moose are known to persist in other landscapes modified by humans such as clear-cuts and agricultural areas within forested landscapes (Schneider and Wasel 2002 Rempel et al. 1997, Leptich and Gibert 1989), the agricultural-dominated landscape of the northern Great Plains represents a unique habitat for the species that was not inhabited by moose prior to human-induced habitat change. Moreover, while numerous prior efforts have provided insight into moose movements and resource use in traditional habitats (e.g. Labonte et al. 1998, MacCracken et al.1997, Cederlund and Sand 1994, Leptich and Gilbert 1989, Kearney and Gilbert 1976), the ecology and behavior of moose in the prairie ecoregions of North America is entirely unknown.

The purpose of this project was to investigate the ecology of moose in both traditional woodland habitats and the recently colonized prairie region of North Dakota, including investigating how this species may be taking advantage of landscape alterations to extend its range. The specific objectives were to (1) examine seasonal and annual
movements and habitat use of moose in the drift prairie coteau and woodland regions of North Dakota, (2) investigate the diet of moose in the drift prairie coteau and woodland regions of North Dakota, and (3) compare movements, habitat use, and diets of moose in these two regions.

Methods

Study Area

The primary study areas for this part of the project are the Lonetree Wildlife Management Area (WMA) in central North Dakota (47°30' N, 100°15' W) and the Turtle Mountains in north-central North Dakota (48°57' N, 99°53' 00" W; Figure 3). Lonetree WMA is a large wildlife management area, encompassing 134 km² in the prairie-coteau region of the state. Habitats on Lonetree WMA include native mixed grass prairie, corn (Zea mays) or sunflower (Helianthus annuus) food plots (ranging from 6-31 ha in size), numerous seasonal and semi-permanent wetlands, small impoundments along the Sheyenne River, and planted woodlands in the form of linear tree rows or larger block plantings (Smith et al. 2007). The area surrounding the Lonetree WMA is comprised primarily of pasture and hay land as well as crop fields consisting predominantly of small grains. Planted tree rows and woodlots are also present with some natural woodlands occurring in woody draws along the Missouri Escarpment that marks the border between the Northern Glaciated Plains and Missouri Coteau ecoregions (U.S. Environmental Protection Agency 1996). Typical grassland plants found in the Lonetree WMA area include prairie junegrass (Koeleria macrantha), indiangrass (Sorghastrum nutans), needle and thread grass (Hesperostipa comata), brome (Bromus spp.), wheat grass (Agropyron spp.) and alfalfa (Medicago sativa). Common tree species in planted and or native

Figure 3. Location of the Lonetree Wildlife Management Area and Turtle Mountains study areas in North Dakota, USA. Boundaries delineate North Dakota counties.

The Turtle Mountains are located along the Canadian border and are characterized by hilly wooded terrain and numerous small lakes and wetlands with interspersed agricultural fields, pasture land, and hay fields, especially near the southern edge of the area. The forest of the Turtle Mountains is comprised primarily of aspen and bur oak along with green ash and paper birch (*Betula papyrifera*), balsam poplar (*Populus balsamea*), and box elder, with an understory of chokecherry, hazel (*Corylus cornuta*),

**Moose Collaring Operations**

In January 2004-2006 global positioning system (GPS) collars (Lotek Wireless Inc. Newmarket, Ontario, Canada) were placed on 14 adult moose (6 in the Lonetree WMA, 8 in the Turtle Mountains). In 2004, only moose in the Lonetree WMA study area were captured, but in 2005 and 2006, the study was expanded to include the Turtle Mountains area. Moose were captured by helicopter with the use of a net gun. Collaring operations were performed by Leading Edge Aviation, Lewiston, ID. Collars were set to acquire a location every 4 hours, and location data were stored on board. After approximately 52 weeks, collars were recovered when moose were recaptured or after they automatically dropped off via timed-release mechanisms. Collared moose were periodically monitored by aerial and ground-based VHF telemetry to determine their general whereabouts and monitor collar function and animal health. All study animals surviving the previous year were fitted with new collars during subsequent capture operations.

**Home Range Estimation**

Annual and seasonal moose home range sizes (km$^2$) were estimated with a 95% fixed-kernel estimator, with seasons defined as winter (January-April), summer (May-August), and fall (September-December) for all analyses. The fixed-kernel estimator is a
bivariate function that calculates a probability density distribution around each X, Y location in a grid and sums these distributions to create a probability density distribution for the entire sample of points. Home range is delineated by generating contours that define a certain percentage of the distribution within which there is a certain probability of the animal being located (typically 95%) (Worton 1989).

Several past researchers have emphasized the importance of maximizing the number of observations in telemetry studies in order to retain biological relevance as opposed to eliminating locations to reduce serial independence (De Solla et al. 1999, McNay et al. 1994, Poole and Smith 2006, Rooney et al. 1998), Additionally, the removal of locations does not necessarily guarantee a reduction in autocorrelation (De Solla et al. 1999, Rooney et al. 1998), and in the case of my data, experimental removal of points to as few as one location per week did not reduce autocorrelation based on the Swihart and Slade index (Swihart and Slade 1985). Therefore, I carried out home range calculations using all available locations for non-dispersing moose, with dispersal defined as locations for a moose that deviated from other grouped relocations for that animal (Dodge et al. 2004). Seasonal home range sizes were estimated for each moose for all seasons for which at least 30 locations were available, and annual home ranges were estimated for moose with at least 30 locations in every season (Seaman et al. 1999). Moose were considered to exhibit seasonal migrations if less than 25% of their seasonal home ranges overlapped (Dodge et al. 2004). Location data were input in to ArcMap 9.2 (ESRI Inc., Redlands, California, USA), and home range calculations were performed using the Home Range Extension (Rodgers and Carr 1998). I compared annual home range sizes between study sites with a Welch's two-sample t-test. I also compared home range sizes between study sites with a Welch's two-sample t-test.
range sizes between seasons and study sites with repeated-measures ANOVA. When necessary, home ranges were natural log transformed to meet the assumptions of parametric tests. All statistical comparisons were performed in the statistical package \( R \) (The R Foundation for Statistical Computing, Version 2.6).

\textit{Habitat Use}

Habitat use and habitat preference were determined by plotting moose locations onto a geographic information system (GIS) map of available habitat types and comparing observed moose habitat use to expected use based on habitat availability. Because any individual moose could not use all possible habitats within the state, it was first necessary to first determine the area available to each moose at each study site. As opposed to the 95\% often used for home range studies, I constructed 99\% fixed-kernel home ranges for each moose and then combined the home ranges for each study site into a single polygon which defined the area available to moose at that study site. I chose a 99\% kernel to maximize the probability that I included all habitats potentially used by moose in the two study areas.

I then used land cover data from the United States Geological Survey’s Gap Analysis Program (GAP) compiled from 1992-1999 (Strong et al. 2005) to determine habitat types available to moose. To make the comparison of habitat use between study sites possible, land cover data were collapsed to four habitat types using Spatial Analyst in ArcMap 9.2 (ESRI Inc., Redlands, California, USA). These were defined as woodland (all planted and naturally occurring woodlands), wetland (temporary, seasonal, permanent, and semi-permanent wetlands), grasslands (planted non-native grasses, hay fields, old fields, and planted or naturally occurring prairie), and crops (all planted row
crops or grains). I then clipped habitat layers to the extent of the polygons delineating the area available to moose at each study site. Next, because preliminary analysis indicated that the coarse spatial resolution (30 m) of the GAP data was insufficient to detect small areas of habitat, I improved the resolution of terrestrial habitat layers by redigitizing them based on 1-m resolution aerial photos of each study site (National Agricultural Imagery Program, USDA-NRCS 2005). To determine the availability of wetland habitats, I used National Wetland Inventory 1:24,000 digital quadrangles (U.S. Fish and Wildlife Service 2000). Because preliminary results indicated that I may have overestimated the amount of wetland habitat actually available to moose, I adjusted the wetland habitat layer by considering all temporary and seasonal wetlands to be part of the terrestrial habitat in which they were imbedded, as these wetland are typically inundated only during the spring and do not provide a source of emergent or submergent aquatic vegetation (U.S. Fish and Wildlife Service 2000). I also adjusted wetland habitat availability to account for the presence of several larger lakes in the two study areas. Because the deep water areas in these lakes were unlikely to be available to moose, I created a buffer layer that extended from the shoreline 100 meters into each lake. This distance was chosen as a conservative estimate of the extent of the littoral zone, where water depth was shallow and emergent and submergent plants would occurred. The area of this buffer layer was considered the amount of lake habitat available to moose. The area of each habitat polygon in each study area was then measured using the X-Tools extension for ArcMap 9.2 (ESRI Inc., Redlands, California, USA).

All locations for individual moose at each study site were separated into seasons. Resource selection functions (RSFs) were calculated for each moose for all seasons for 20
which a minimum of 30 locations were available for that animal. An RSF refers to any one of a broad class of analyses aimed at quantifying differential resource selection by animals. RSFs are usually calculated to compare the use of resource categories versus how available they are on the landscape or to determine the use of particular resource classes versus the non-use of others (Manly et al. 2002). In this study, to calculate RSFs the area of available habitat types in each study areas were first normalized to a proportion, with the proportions of all habitats summing to one (Manly et al. 2002). Habitat selection was then calculated separately for each moose as the proportion of total seasonal or annual locations in a particular habitat type divided by the proportional availability of that habitat type. This resulted in RSF coefficients that represented the probability of a moose using a particular habitat if all habitats were equally available (Manly et al. 2002, Osko et al. 2004). Because there were four habitat types, selection for a particular habitat type would be indicated by an RSF coefficient of greater than 0.25. I compared habitat selection with a multivariate MANOVA to examine any differences in habitat use between study area and season (McLoughlin et al. 2002, Osko et al. 2004). I then used repeated-measures ANOVAs with study area and season as factors to examine how use of specific habitat types differed between study areas and seasons, respectively. Tukey’s post hoc tests were used to examine pairwise differences in habitat use between seasons. Prior to analyses, RSF coefficients were arcsine transformed to meet the assumptions of parametric tests.

*Fixed-Kernel Smoothing Parameters*

While the kernel function determines the shape of the distribution around each point, the smoothing parameter determines the widths of the distributions. A smaller
smoothing parameter will produce more detailed contours for the density distribution, while a larger smoothing parameter will produce more smoothed contours obscuring some of the detail of the distribution (Silverman 1986). Although least squares cross validation (LSCV) is the most frequently recommended technique to determine the optimal smoothing parameter, or bandwidth, for fixed-kernel home range estimation (Seaman and Powell, Seaman et al. 1999, Worton 1995), this technique may fail to calculate a smoothing parameter, particularly when there are a large number of locations (Hemson et al. 2005). Also, when there are clusters of locations in close proximity to each other, LSCV may produce a smoothing parameter that is too small, resulting in dramatic under-smoothing of the home range estimate (Hemson et al 2005, Silverman 1986). In the case of my data, both of these problems were encountered, as LSCV was unable to calculate a smoothing parameter for most sets of locations, and when it did, the multi-modal nature of moose locations produced home ranges that were dramatically under-smoothed. In contrast, similar to prior studies (Seaman and Powell 1996, Seaman et al. 1999), use of the other commonly employed smoothing parameter, the reference parameter (h_ref) (Worton 1989), appeared to over-smooth home ranges, resulting in over-estimates of home range size. To deal with these problems, I used biased cross validation (BCV) to calculate the smoothing parameters for all fixed-kernel home range estimations (Rodgers and Carr 1998, Wand and Jones 1995). The use of BCV avoided the problems associated with LSCV while smoothing home range estimates less than using h_ref did. Although BCV has not been commonly applied to estimate the smoothing parameters for home range estimates, the statistical literature has demonstrated its utility
in selecting kernel bandwidth, as well as its potential superiority to LSCV (Rodgers and Carr 1998, Sain et al. 1994, Wand and Jones 1995).

**Moose Diets**

To determine the feeding habits of moose at Lonetree WMA and the Turtle Mountains, I collected samples of fresh moose feces for microhistological-based diet estimates (Van Vuren 1984). Five samples a month were collected by haphazardly searching several locations distributed across each study site, with no more than two samples per month collected from a single location. Samples were combined to generate a series of two-month composite fecal pellet samples. Fecal pellets were sent to the Diet Analysis Laboratory at Washington State University, Pullman, Washington, USA for microhistological determination of plant fragments and estimates of diets to the genus and species level. Forage plants were classified into five categories: woody browse, grasses and sedges, forbs, crops, and other (fruits, nuts, aquatic vegetation). Results of diet analysis were then grouped into seasons based on the same criteria used for home range and habitat use analyses.

**Results**

**Mortality of Collared Moose**

Three radio collared bull moose and one radio collared cow died during the study period. In December of 2004 an adult cow moose (No. 200) was found dead in a cornfield near the Lonetree WMA. A field examination determined that the animal had been shot illegally. In October of 2005, a telemetry flight conducted by the North Dakota Game and Fish Department detected the mortality signal on the collar of a bull moose (No. 194) in the Turtle Mountains. The carcass of this bull moose was located from the
ground the following week, but the carcass was scavenged and partially decomposed, thereby making it difficult to definitively assign a cause of death. However, evidence around the carcass suggested the animal had lain on its side in one position while kicking out with its legs for some time prior to death. These observations suggested the moose had been sick or infected with meningeal worms, and eventually died as a result. In April 2006, a collared bull moose (No. 151) was found dead by a farmer northeast of the Lonetree WMA. The presumed cause of death for this animal was a heavy winter tick (*Dermacentor albipictus*) infection. In June 2006 a dead collared bull moose (No. 156) was located via aerial telemetry roughly 16 km north of Bottineau, ND. The cause of death is unknown as this animal was heavily scavenged.

*Moose Movements*

Data from the original GPS collars deployed in both study areas were analyzed to examine the movements and home ranges of these moose. Unfortunately, a high rate of collar failure in 2005 prevented the calculation of all seasonal and annual home ranges. One adult cow moose dispersed from the Lonetree WMA in March 2004. Locations for this cow moose revealed that it had traveled as far as 90 km from the original capture location. When the collar on this cow moose failed in September 2004, the animal had established a home range in the region northwest of Butte, ND, approximately 56 km from Lonetree WMA. This moose was captured and re-collared in 2005 and remained in this area for the remainder of the time that his radio collar functioned. Based on their locations, none of the radio collared moose exhibited seasonal migrations.

*Home Range*

The remaining five animals collared in the Lonetree study area remained in the general vicinity of Lonetree WMA. Among the eight moose that were captured and
monitored in the Turtle Mountains study area, GPS radio collars were recovered from seven animals. I was unable to recover the radio collar from the eighth animal, and believe that this GPS radio suffered a total failure. All of the animals for which GPS location data were available remained in the Turtle Mountains area. Unfortunately, however, three of the seven recovered collars ceased collecting location records prematurely, limiting my analyses of habitat use and movements by moose in the Turtle Mountains area to the winter period.

Estimates of annual home range size based on the 95% fixed kernel method ranged from 59.2 to 262.6 km² for moose in the Lonetree study area, which was larger than home range movements by moose in the Turtle Mountains study area (9.6-47.7 km²; \(t_{5.3} = 3.7, P = 0.01\), mean number of locations = 2709; Table 1, Figure 4). Seasonal home range estimates varied from 18.8 to 292.8 km² for Lonetree moose and from 1.0 to 44.7 km² for Turtle Mountains moose (Table 1). Seasonal home ranges were also larger for Lonetree moose (\(F_{1,25} = 13.3, P = 0.0012\), mean number of locations = 807; Figure 4). Home range size did not differ greatly among seasons at either study site (\(F_{2,25} = 0.1, P = 0.91\); Table 1). One moose (Table 1) was excluded in statistical comparisons of seasonal home range size because although there were greater than 30 locations for this animal, they all occurred within a 1-month time frame. Also, because locations for all seasons were available for only one male in each study site, I did not compare male and female home ranges.

_Habitat Use_

Availability of each of the four habitat types for the Lonetree and Turtle Mountains study areas is shown in Table 2. Results of habitat use analyses indicated that
Moose in both study areas showed a strong selection for wooded habitat in all seasons (Table 2). Moose in the Turtle Mountains also selected wetland habitats during the summer, but moose did not select for cropland or grassland habitats in either study site (Table 3). The MANOVA results indicated that moose habitat use differed between study area and by season (Table 4). Results of repeated measure ANOVAs examining differences in the use of specific habitat types revealed that while moose in both study areas selected for woodlands, selection was stronger for Lonetree moose (Table 5, Figure 3). Moose in the Turtle Mountain area utilized wetland and grassland habitats more than Lonetree moose, whereas use of cropland habitats did not differ between sites (Table 5, Figure 5). Moose used woodland habitats more in winter than in spring or summer (Table 5, Figure 6). Moose also selected for wetlands more in summer and fall than in winter, and selected for croplands more in fall than in other seasons (Table 5, Figure 6). Use of grassland habitat did not vary among seasons (Table 5, Figure 6).

Table 1. Seasonal (Winter, Summer, Fall) and total home range estimates (km²) for moose in the Lonetree and Turtle mountains study areas based on the 95% fixed-kernel estimator.

<table>
<thead>
<tr>
<th>Study Area</th>
<th>Moose</th>
<th>Sex</th>
<th>Winter</th>
<th>Summer</th>
<th>Fall</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lonetree</td>
<td>151</td>
<td>Male</td>
<td>58.3</td>
<td>35.7</td>
<td>99.7</td>
<td>100.1</td>
</tr>
<tr>
<td></td>
<td>195</td>
<td>Female</td>
<td>277.3</td>
<td>292.8</td>
<td>210.9</td>
<td>262.6</td>
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<tr>
<td></td>
<td>197</td>
<td>Female</td>
<td>293.7</td>
<td>172.6</td>
<td>200.6</td>
<td>236.0</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>Female</td>
<td>18.8</td>
<td>157.2</td>
<td>115.6</td>
<td>144.4</td>
</tr>
<tr>
<td></td>
<td>203</td>
<td>Female</td>
<td>47.0</td>
<td>28.7</td>
<td>80.8</td>
<td>59.2</td>
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<td></td>
<td>271</td>
<td>Female</td>
<td>22.1</td>
<td>20.9</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>Turtle Mountains</td>
<td>192</td>
<td>Male</td>
<td>44.2</td>
<td>16.1</td>
<td>39.1</td>
<td>42.6</td>
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<tr>
<td></td>
<td>156</td>
<td>Male</td>
<td>19.3</td>
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<td>na</td>
<td>na</td>
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<tr>
<td></td>
<td>189</td>
<td>Male</td>
<td>22.2</td>
<td>na</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td></td>
<td>194*</td>
<td>Male</td>
<td>1.0</td>
<td>na</td>
<td>na</td>
<td>na</td>
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<tr>
<td></td>
<td>188</td>
<td>Female</td>
<td>19.5</td>
<td>28.1</td>
<td>30.4</td>
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<td>190</td>
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<td>9.6</td>
</tr>
<tr>
<td></td>
<td>193</td>
<td>Female</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
</tr>
</tbody>
</table>

*This animal was not included in statistical comparisons of seasonal home range size.
Figure 4. Mean annual and seasonal home range sizes (±S.E.) based on 95% fixed kernel home range estimates for GPS-collared moose in the Lonetree and Turtle Mountain study areas.

Table 2. Proportional availability of each of the four major habitat types in the Lonetree and Turtle Mountains study areas.

<table>
<thead>
<tr>
<th></th>
<th>Woodland</th>
<th>Wetland</th>
<th>Grass</th>
<th>Crop</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lonetree</td>
<td>0.025</td>
<td>0.053</td>
<td>0.400</td>
<td>0.522</td>
</tr>
<tr>
<td>Turtle Mountains</td>
<td>0.451</td>
<td>0.170</td>
<td>0.252</td>
<td>0.127</td>
</tr>
</tbody>
</table>

Table 3. Resource selection function (RSF) coefficients for four habitat types based on data from 13 GPS-collared moose in the Lonetree and Turtle Mountains study areas. Bold numbers indicate positive selection (> 0.25) for a habitat type.

<table>
<thead>
<tr>
<th>Study Site</th>
<th>Season</th>
<th>n</th>
<th>Woodland</th>
<th>Wetland</th>
<th>Crop</th>
<th>Grassland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lonetree Winter</td>
<td>6</td>
<td>0.95</td>
<td>0.013</td>
<td>0.013</td>
<td>0.024</td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>6</td>
<td>0.89</td>
<td>0.048</td>
<td>0.024</td>
<td>0.034</td>
<td></td>
</tr>
<tr>
<td>Fall</td>
<td>5</td>
<td>0.84</td>
<td>0.067</td>
<td>0.051</td>
<td>0.038</td>
<td></td>
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<tr>
<td>Turtle Mountains</td>
<td>Winter</td>
<td>7</td>
<td>0.76</td>
<td>0.16</td>
<td>0.031</td>
<td>0.048</td>
</tr>
<tr>
<td>Summer</td>
<td>4</td>
<td>0.56</td>
<td>0.30</td>
<td>0.015</td>
<td>0.13</td>
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</tr>
<tr>
<td>Fall</td>
<td>4</td>
<td>0.54</td>
<td>0.21</td>
<td>0.10</td>
<td>0.15</td>
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</tr>
</tbody>
</table>
Table 4. Results of multivariate MANOVA comparison of moose habitat selection between study site and season for GPS-collared moose in the Lonetree and Turtle Mountain study areas.

<table>
<thead>
<tr>
<th></th>
<th>df</th>
<th>Pillai's trace</th>
<th>F</th>
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<tr>
<td>Site</td>
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<td>0.84</td>
<td>30.9</td>
<td>&lt;0.0001</td>
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<tr>
<td>Season</td>
<td>2</td>
<td>0.82</td>
<td>4.2</td>
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</tr>
<tr>
<td>Site x Season</td>
<td>2</td>
<td>0.28</td>
<td>0.98</td>
<td>0.46</td>
</tr>
</tbody>
</table>

Table 5. Results of repeated measures ANOVAs comparing selection of four habitat types by site and season for GPS collared moose in the Lonetree and Turtle Mountain study areas.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>F</th>
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<th>df</th>
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</thead>
<tbody>
<tr>
<td>Site</td>
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<tr>
<td>Wood</td>
<td>82.2</td>
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<tr>
<td>Wet</td>
<td>81.4</td>
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<tr>
<td>Crop</td>
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<tr>
<td>Grass</td>
<td>7.0</td>
<td>0.013</td>
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<tr>
<td>Season</td>
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<td></td>
<td></td>
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<tr>
<td>Wood</td>
<td>12.5</td>
<td>0.00013</td>
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</tr>
<tr>
<td>Wet</td>
<td>6.8</td>
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<td>2</td>
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<tr>
<td>Crop</td>
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<td>0.011</td>
<td>2</td>
</tr>
<tr>
<td>Grass</td>
<td>2.5</td>
<td>0.10</td>
<td>2</td>
</tr>
</tbody>
</table>

Figure 5. Mean habitat selection indices (+ S.E.) for GPS-collared moose in the Lonetree and Turtle Mountain study areas. Values greater than 0.25 indicate selection for a particular habitat whereas values less than 0.25 suggest avoidance. Bars marked with an asterisk indicate a significant difference in habitat use based on repeated measures ANOVAs comparing the use of each habitat type by site and season.
Figure 6. Mean habitat selection indices (+ S.E.) for GPS-collared moose in winter (January-April), summer (May-August), and fall (September-December). Values of greater than 0.25 indicate selection for a particular habitat whereas values less than 0.25 suggest avoidance. Seasonal selection of each habitat did not differ for bars labeled with the same letter, based on Tukey’s post-hoc comparisons.

Moose Diets

Results of diet analyses indicated that moose consumed predominately woody plants in both the Lonetree (≥65%) and Turtle Mountains (≥83%) study areas in all seasons of the year (Figure 7). Woody browse consumption was particularly high among moose in the Turtle Mountains study area. During winter periods for example, moose in the Turtle Mountains consumed 99% woody browse, which was primarily aspen (36%) and willow (20%). Willow and aspen were also important components of the diets of moose in the Turtle Mountains during summer (15% and 12%, respectively) and fall (19% and 23%). Bur oak stems and leaves were also common items in these seasons, making up 20% of summer and 23% of fall diets. At the Lonetree study area Russian olive was the most common woody plant species eaten by moose in all seasons, and this diet component made up 50% of fall diets. Willow (10% of summer diets) and
Figure 7. Seasonal diet composition (%) of moose in the Lonetree and Turtle Mountains study areas.
cottonwood (11% of winter diets) were the next most common browse species for moose in the Lonetree study area. Row crops (primarily corn), were also a major component of the diets of moose in the Lonetree area during the fall (11%) and winter seasons (22%; Figure 5). In contrast, row crops were absent from samples collected in the Turtle Mountains study area, although alfalfa was an important component of the diets of Turtle Mountains moose in summer (13%) and fall (13%) making up the 90% of the forbs consumed during these periods. Grasses (≤3%) and fruits and nuts (≤1%) were minor components of moose diets in both study areas, while emergent and submergent aquatic vegetation made up ≤1% of moose diets during the open water period of summer and fall.

**Discussion**

**Sample Size and GPS Collar Performance**

The small sample sizes of collared moose were the result of some of the limitations encountered in conducting this study. For example, the low density of moose in the Lonetree area limited the number of animals that could potentially be collared there. During the first year of the study (2004), collars were placed on all five of the moose known to be in the vicinity of the Lonetree WMA based on observations by biologists in fixed-wing aircraft. Over the next several years of the study, capture operations succeeded in fitting radio collars to nearly all moose in the Lonetree study area. The unanticipated poor performance of the Lotek GPS radio collars placed on moose during the study limited many of my planned analyses and contrasts between moose in their traditional range and in the prairie coteau area. Overall, nearly half of the 22 radio collars that were deployed failed prematurely. Six of the ten collars (60%) placed on animals in the Turtle Mountains study area failed, including four of five collars
deployed in 2005. Despite these small sample sizes, the data and analyses that were possible have provided valuable new information on the ecology of moose in North Dakota.

*Migration and Dispersal*

My results suggest that the moose I collared in North Dakota are non-migratory. This finding was unusual because prior research has found that moose typically migrate between seasons to avoid deep snows and to take advantage of seasonally available forage across the landscape (Ballard et al. 1991, Hundertmark 1998, Poole and Stuart-Smith 2006). However, moose range in North Dakota lacks the differences in elevation that result in great variability in snowfall amounts, and while conifer forests may serve as thermal cover or to reduce snow depth in other areas where moose occur (Pierce and Peek 1984, Thompson and Stewart 1998), these habitats are not present in North Dakota. Additionally, habitat selection and diet composition of moose in both study areas indicated that moose do not exhibit dramatic seasonal shifts in diet or habitat use, as moose selected for wooded habitats and consumed primarily woody browse in all seasons. Where changes in selection did occur, such as the increased use of cropland in fall (Figure 4), the heterogeneous nature of the landscape in the different study areas may have eliminated the need for moose to move long distances to gain access to seasonally preferred forage items (e.g. corn).

One radio collared moose that was captured in the Lonetree WMA dispersed a distance of approximately 56 km to the northwest of Lonetree WMA. Although it is unclear what triggered this movement, dispersal of moose from their natal range is not uncommon. Although dispersal distances for moose are typically short such that adult
home ranges often overlap with the natal home range, dispersal distances of > 50 km have previously been reported for both young and adult cow moose (Cederlund et al. 1987, Mytton and Keith 1981, Ballard et al. 1991). All other radio collared moose remained in the general vicinity of where they were initially captured.

Home Ranges

It is problematic to attempt direct comparisons of movement behaviors by moose from my study to those from previous studies because of differences in the number of locations collected and in the methods used to estimate home range size. However, annual home ranges of moose in the Turtle Mountains ($\bar{x} = 27.7$ km$^2$, SE = 10.0) were well within the range reported for other non-migratory moose in southern parts of the range of the species (Maine, Michigan, Minnesota, New York, and Ontario), which ranged from 2 km$^2$ up to 43 km$^2$ (Addison et al. 1980, Dodge et al 2004, Garner and Porter 1990, Leptich and Gilbert 1989, Phillips et al. 1973). While Turtle Mountains and Lonetree moose exhibited some overlap in home range size, particularly in winter, Lonetree moose demonstrated the potential to possess large home ranges ($\bar{x} = 160.5$ km$^2$, SE = 38.9) that approach the extent of those observed for non-migratory moose in Alaska and the Northwest Territories (174-290 km$^2$; Ballard et al. 1991, Grauvogel 1984, Stenhouse et al. 1994). Home range size is expected to be a function of the energetic requirements of an animal and the spatial distribution of necessary resources (Elchuk and Weibe 2003, McNab 1963, Mitchell and Powell 2004). Thus, where required resources are widely dispersed, home range size will be larger. For example, Ballard et al. (1991) concluded that the large home range sizes they observed were partially the result of the high proportion of unusable habitat (glaciers, high elevation areas) relative to preferred
habitats in their study area. A similar scenario may have produced the relatively large annual home ranges exhibited by Lonetree moose. Although no habitat types were completely unusable by Lonetree moose, the majority of the study area (92%) was composed of grasslands and croplands that moose used less than expected, while only 2.5% of the study area was covered by woodlands, which generally occurred in relatively small patches scattered across the landscape. Because preferred woodland habitats are widely distributed within a larger matrix of less suitable habitat types, moose occupying the prairie-coteau region of North Dakota may need to move over larger areas to acquire sufficient forage resources for survival and reproduction. In contrast, the higher proportion of woodland habitat (45.1%) in the Turtle Mountains resulted in correspondingly smaller home ranges.

Although I did not observe significant differences in home range size between seasons, seasonal home-range size was considerably variable among individual moose (Table 1). Seasonal home range size is thought to vary as a result of seasonal changes in the limiting factors faced by moose (Addison et al. 1980, Doerr 1983, Dussault et al. 2005, and Lynch and Morgantini 1984, Phillips et al 1973). In some cases, energy constraints associated with moving through deep snow or the need to avoid predators may limit moose movements during winter (Dussault et al. 2005, Phillips et al. 1973, Thompson and Vukelich 1981). In warm seasons, or where deep snow is not present, the seasonal availability of suitable forage is more likely to influence seasonal home range size (Doerr 1983, Leptich and Gilbert 1989, Lynch and Morgantini 1984). In North Dakota, moose exist in the absence of established populations of large predators (wolves and bears), and winter snows typically do not exceed depths considered limiting to moose.
Because of this it would be expected that seasonal home ranges would be determined by the distribution of seasonally important resources. As such, differences in the seasonal home-ranges sizes of individual moose in this study likely reflected the spatial pattern of available seasonal resources where these moose resided.

**Habitat Use and Diet**

While the characterization of habitat types in this study was fairly general in order to facilitate comparisons between study sites, the results of habitat selection analyses nevertheless provide important insight into how moose are utilizing available habitats in North Dakota. Numerous researchers have demonstrated the importance of a variety of types of woody habitats in providing forage and/or cover for moose (Peek 1998, Peek et al. 1976, Peterson et al. 1995). Therefore, it was not surprising that moose in North Dakota exhibited a strong selection for woody habitats in all seasons in both study areas. In Minnesota and many areas of Canada, moose inhabit early-successional forests stages that were historically created by periodic fire or insect outbreaks and are now maintained by logging (Peek et al. 1976, Peterson 1955, Phillips et al. 1973). The forests that cover nearly half of the Turtle Mountains study area represent this “typical” moose habitat, yet the tree plantings on and around the Lonetree WMA, although more scattered across the landscape, also appear to provide important habitat for moose.

Given that the consensus among past researchers is that moose habitat use is primarily related to forage availability, especially in the absence of limiting factors such as predators or deep snows (Dussault et al. 2005, Peek 1998), it seems likely that moose use of woodlands in this study was related largely to food resources. However, captive
moose are known to require wind beaks (Franzmann 1998), and moose in my study, particularly in the Lonetree area, may have sought wooded cover to avoid strong winds that occur in the open habitats of North Dakota. Nonetheless, the dominance of woody browse in the diets of moose from both study sites supports the idea that woodland habitats are critical because of the forage they provide. Moose rely on woody habitats because their dietary physiology requires the consumption of palatable browse provided by the leaves and stems of numerous species (Belovsky 1981, Renecker and Schwartz 1998). Moose diets in the Turtle Mountains consisted in large part of browse species, such as aspen, willow, birch, Juneberry, and cherry, that are typically considered major food items for moose. In addition to supporting many of these traditional browse species, the Turtle Mountains also contain an abundance of bur oak, and this species also constituted a major part of summer and fall moose diets. In the Lonetree area, with the exception of willow, the most common woody plants are not typical of those found in traditional moose range, and this was reflected in the diets of Lonetree moose. Russian olive, a shrub commonly found in tree plantings, was the most abundant browse item overall, and two other commonly planted trees, green ash and box elder, made up approximately 11% of winter and summer diets. Thus, the diets of moose in both study areas not only reflect the importance of woodland habitat to moose, but also demonstrate that North Dakota moose are taking advantage of a variety of woody species beyond those encountered in typical moose range.

Although moose did not select for habitats besides woodlands, seasonal changes in the use of croplands and wetlands as well as diet results suggest that moose were taking advantage of seasonally available resources present in other habitat types. Thus,
RSFs may not entirely reflect the importance of habitats besides woodlands. For example, while moose selected against grassland habitats in both study areas, in the Turtle Mountains 13% of summer and fall diets consisted of alfalfa found in hay fields in the area, indicating that this forb was an important supplemental food item during certain times of the year.

Likewise, moose selected against croplands in all seasons, even though cropland use was significantly greater in fall than during other times of the year, and corn was an important part of the fall and winter diets of Lonetree moose. This apparent lack of selection may have been the result of the composition of croplands in the two study areas. Crops in Turtle Mountains consisted almost entirely of small grains (wheat, barley) that were not expected to serve as moose forage, and in Sheridan and Wells Counties, where Lonetree WMA is located, approximately 26% of the total land area was planted in wheat and barley in 2005, while only 2% was corn and 3% was sunflowers (USDA National Agriculture Statistics Service 2005). In contrast, if habitat selection analyses were confined to the boundary of the Lonetree WMA, where the only croplands present were corn and sunflower food plots, then moose would actually show an overall positive selection for cropland habitats (0.29). Therefore, while moose did not select for croplands in general, certain cropland habitats are likely important to prairie moose as a seasonal food source.

I also observed an increase in wetland use by moose during summer and fall, which was primarily driven by Turtle Mountain moose, as use of wetlands was low in all seasons for Lonetree moose (Table 3, Figure 6). However, the increased use of wetlands did not appear to be reflected in moose diets, as aquatic vegetation was apparently a
minor component (≤1%) of summer and fall moose diets in both study areas. However, although aquatic plant tissue was uncommon in moose fecal samples, these plants may still be an important component of moose diets. Moose likely utilize aquatic plants because they provide a highly digestible food source (MacCraken et al. 1993). This high digestibility may have resulted in limited evidence of these plants in moose fecal samples and the subsequent underestimation of their use by moose in this study. Alternatively, moose may utilize aquatic plants because they provide critical minerals not found in terrestrial forage (Belovsky and Jordan 1981, De Vos 1958). However, past research supporting this idea was conducted in boreal habitats with thin, nutrient-poor soils (Belovsky and Jordan 1981). In contrast, North Dakota soils are more nutrient rich and tend to be saline or sodic (Seelig 2000). As a result, terrestrial forage in North Dakota may contain sufficient quantities of minerals such as sodium, potentially eliminating the need for aquatic plants to make up a large proportion of moose diets. Increased wetland use in summer and fall by moose in this study, may therefore have been independent of forage requirements and instead triggered by the need to thermoregulate, or avoid insects (Belovsky and Jordan 1981, De Vos 1958).

In summary, the combined results of home range, habitat use and diet analyses provide insight into the factors influencing space use by moose in both traditional and prairie habitats in North Dakota. While woodland habitats appear to be critical for moose throughout their range in North Dakota, other seasonally available resources such as corn and alfalfa may provide a supplemental food source, while wetlands may help moose meet physiological needs. Further, these results strongly support the hypothesis that
mOOSE range expansion is the direct result of landscape modifications, particularly the creation of woody habitat, occurring since European settlement.

Management Implications

This study represents the first of its kind in North Dakota, and should provide managers with valuable information regarding the ecology of moose in traditional and more recently colonized habitats of the state. While moose have expanded their range to include areas of North Dakota that were traditionally prairie, the woodland habitats that they depend on still make up a very small proportion of the overall landscape in these areas, thereby requiring moose to range over large home ranges to acquire sufficient resources. As a result, managers should be aware that prairie habitats are likely capable of supporting fewer moose than forested areas and that the continued persistence of prairie populations of moose will be dependent on the maintenance of wooded habitat for this population. Additionally, my results suggest that the planted woodlands and food plots of the Lonetree WMA may be making this area particularly attractive to prairie moose, and the continued management of this area to provide food and cover for wildlife may allow it to continue to support a local moose population.
CHAPTER III
GIANT LIVER FLUKE (FASCIOLOIDES MAGNA) AS A POTENTIAL MORTALITY FACTOR FOR NORTH DAKOTA MOOSE: HISTORICAL PREVALENCE, CURRENT OCCURRENCE, AND INTERMEDIATE HOST AVAILABILITY

Introduction

White-tailed deer (Odocoileus virginianus) are the normal host for two parasites that may cause fatal disease in moose (Alces alces). The most well-known of these is the meningeal worm (Parelaphostrongylus tenuis), a nematode long implicated as a limiting factor for moose populations (Dumont and Crete 1996, Gilbert 1973, Whitlaw and Lankester 1994). The other is the giant liver fluke (Fascioloides magna), a large trematode that occurs in pairs or groups within fibrous capsules in the liver parenchyma of its normal hosts, white-tailed deer and elk (Pybus 2001). F. magna has an indirect life cycle, requiring aquatic snails of the genus Lymnaea (hereafter Lymnaeid snails) to serve as intermediate hosts (Pybus 2001). In dead-end hosts such as moose, juvenile flukes migrate much more extensively than in normal hosts before becoming encapsulated, causing considerable destruction of liver tissue (Pybus 2001). Extensive fibrosis as a result of the migratory tracts and capsules containing adult flukes can result in damage to 50-90% of the liver, sometimes resulting in death of the host (Aho and Hendrickson 1989, Lankester 1974, Pybus 2001). Recently, F. magna was implicated in a long-term
decline of the moose population in northwestern Minnesota (Figure 8), where 89% of moose examined from 1995-2000 were infected with *F. magna* (Murray et al. 2007).

The North Dakota Game and Fish Department conducts annual winter aerial surveys of moose populations in three survey areas (Turtle Mountains, Drift Prairie and Pembina Hills; Figure 8). Winter aerial survey data collected by the North Dakota Game and Fish Department indicate that while moose populations appear to be stable to increasing in the Turtle Mountains and Drift Prairie areas, moose numbers have declined considerably in the Pembina Hills survey area in the past decade (Johnson 2002, 2007; Figure 9). Because the Pembina Hills area is adjacent to the declining northwestern Minnesota moose population, concern exists that the North Dakota decline may also be related to *F. magna* infection. This study sought to address this concern by (1) examining historical data to estimate past prevalence of this parasite in the state’s moose population, (2) investigating the current occurrence of *F. magna* infection in moose in North Dakota, and (3) determining whether suitable intermediate hosts for this parasite occur in the state.

**Methods**

To estimate the historical prevalence of *F. magna* in North Dakota moose, I reviewed two data sets previously collected by North Dakota Game and Fish Department (NDGF). The first data set consisted of moose hunter check-station records for 158 moose harvested from 1977-1984. During these first eight years of the North Dakota moose season, hunters were encouraged to bring entire carcasses of harvested moose to check stations where the animals were weighed and the viscera examined to assess reproductive status and parasitic infection. The second source of historical data was
necropsy reports for moose dying of non-hunting related causes. As part of targeted surveillance for wildlife diseases, the NDGF wildlife veterinarian conducted full necropsies on 32 such moose from 1983-1992.

Figure 8. Level III ecoregions of northeastern North Dakota and northwestern Minnesota showing the North Dakota moose aerial survey blocks and the primary study area (Agassiz National Wildlife Refuge, Red Lake Wildlife Management Area, Thief Lake Wildlife Management Area, Beltrami Island State Forest) of Murray et al. (2007).

I reviewed check station data sheets and necropsy reports for evidence of liver fluke infection based on the recovery of flukes from liver tissue or comments in reports that suggested fluke infection, e.g. unspecified cysts or capsules, fibrous areas, migratory tracts, liver congestion, necrosis, or “bad” or “questionable” livers. Additionally, examination of the necropsy reports from targeted surveillance allowed me to compare the relative frequency of *F. magna* infection with that of other sources of mortality. A Clopper-Pearson binomial confidence interval was calculated for the historical estimate
of *F. magna* prevalence obtained from the check station and necropsy data (Rosza et al 2000).

![Graph showing moose observations](image)

**Figure 9.** Number of moose observed within three different survey units in North Dakota during winter period aerial surveys by the North Dakota Game and Fish Department from winter 1980 to 2006. Winter period aerial surveys for moose were not completed in the Drift Prairie area before 1987 (data from Johnson 2002, 2007).

I estimated the current occurrence of *F. magna* infection in moose by examining 78 moose livers collected from hunters during the 2002 and 2003 North Dakota moose seasons. Livers were sectioned into approximately 2-cm wide slices and examined for the presence of adult or juvenile *F. magna* and signs associated with *F. magna* infection, e.g. fibrous tissue, migratory tracts, or detritus (Lankester 1974).

I also investigated the occurrence of intermediate hosts for *F. magna* by sampling wetlands, small lakes and streams for Lymnaeid snails during four summer periods (2003 to 2006). I sampled a total of 78 wetlands, small lakes, and streams for the presence of Lymnaeid gastropods at 12 sites (11 in northeastern North Dakota, 1 in northwestern North Dakota).
Minnesota; Figure 10). Each site was sampled by a series of ten 1-meter sweeps with a dip net approximately every 10 m within 1-2 meters of the shore. After each sweep the contents of the net were examined for aquatic gastropods. Also, Lymnaeid snails observed floating on the surface were collected opportunistically. All snails that were recovered during surveys were collected and placed in 70% ethanol or frozen prior to identification. Snails were identified to species using the criteria of Clarke (1973) and Cvancara (1983).

Figure 10. Map of North Dakota moose hunting units and sites where sampling was done for Lymnaeid snails. Closed circles represent sites where sampling detected presence of Lymnaeid snails. Open circles represent sites where sampling failed to detect presence of Lymnaeid snails. Numbers represent number of wetlands from which snails were recovered/ number of wetlands sampled at each site.
Results

Based on the review of check station records and necropsy reports, the historic prevalence of *F. magna* infection in North Dakota moose was 19.5% (95% C.I., 14.1-25.8%, N=190; Table 6). In the 158 hunter-killed moose, there was evidence for *F. magna* infection in 31 (19.6%) animals. Liver flukes were recovered from 18 (11.4%) of these moose, while signs suggesting possible liver fluke infection were observed in another 13 (8.2%) (6 with unidentified cysts, 5 with bad livers; 2 with scar tissue).

Because only the northeastern area of North Dakota (Unit M1C, Figure 9) was open to moose hunting from 1977-1982, 138 of the 158 hunter-killed samples originated from this area. Liver flukes were recovered from 16 (11.6%) of these moose, and signs consistent with fluke infection were observed in another 13 (9.4%). Hunting for moose was initiated in Units M4-M10 in 1983. Liver flukes were recovered from two of the 20 moose that were harvested by hunters from Units M4-M10 in 1983 and 1984 (Table 6).

Table 6. Number of moose showing signs of *F. magna* infection for each of seven units with moose hunting in North Dakota. Data are from examination of 158 hunter-killed animals, and from necropsies that were performed on 32 moose that died of unknown causes (non-hunting-related) from 1977-1993.

<table>
<thead>
<tr>
<th>Unit</th>
<th>Hunter-killed</th>
<th>Non-hunting</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Examined</td>
<td>Infected</td>
<td>Examined</td>
</tr>
<tr>
<td>M1C</td>
<td>138</td>
<td>29(21.0%)</td>
<td>6</td>
</tr>
<tr>
<td>M4</td>
<td>4</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>M5</td>
<td>6</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>M6</td>
<td>5</td>
<td>0</td>
<td>21</td>
</tr>
<tr>
<td>M8</td>
<td>4</td>
<td>2(50.0%)</td>
<td>0</td>
</tr>
<tr>
<td>M9</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M10</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Unknown</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>158</td>
<td>31(19.6%)</td>
<td>32</td>
</tr>
</tbody>
</table>
Necropsy reports for the 32 moose dying of non-hunting related causes showed that six of these animals (18.8%) exhibited pathology suggesting *F. magna* infection (two with liver congestion, one with liver infection, one with fibrosis of the liver, and one with fibrous capsules; Table 6). Cause of death was considered due to *F. magna* infection in only one of these cases. By comparison, 24 (75.0%) moose exhibited signs consistent with *P. tenuis* infection (nematodes, eosinophilia, malacia, and/or perivascular cuffing in cranium). Six moose died of other causes. *F. magna* was not recovered from any of the 78 moose livers we collected in 2002 and 2003, nor were signs characteristic of *F. magna* infection observed in any of these animals. The moose hunting unit of origin was known for 56 of the samples, while the origin of 22 samples was unknown (Table 7).

<table>
<thead>
<tr>
<th>Unit</th>
<th>1977-1993</th>
<th>2002-2003</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1C</td>
<td>144</td>
<td>4</td>
</tr>
<tr>
<td>M4</td>
<td>5</td>
<td>22</td>
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<tr>
<td>M5</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>M6</td>
<td>26</td>
<td>4</td>
</tr>
<tr>
<td>M8</td>
<td>6</td>
<td>16</td>
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<tr>
<td>M9</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>M10</td>
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<td>2</td>
</tr>
<tr>
<td>Unknown</td>
<td>2</td>
<td>22</td>
</tr>
<tr>
<td>Total</td>
<td>190</td>
<td>78</td>
</tr>
</tbody>
</table>

A total of 418 Lymnaeid snails representing three species (*Lymnaea caperata*, *L. elodes*, and *L. stagnalis*) were recovered from ten of the 12 sites and 55 of the 78 total wetlands sampled (Table 8; Figure 10). At the two sites where snails were not collected, only two wetlands were present. All three species collected were known hosts for *F. magna* (Laursen et al. 1989, Foreyt and Todd 1978, Swales 1935). *Lymnaea elodes* was
the most common, occurring at nine sites, while *L. stagnalis* and *L. caperata* were found at five and four sites, respectively (Table 8).

Table 8. Number of individuals of three species of Lymnaeid snails collected and the number of sites where each species was collected during a survey of 78 wetlands at 12 sites (11 in North Dakota, 1 in northwestern Minnesota).

<table>
<thead>
<tr>
<th>Species</th>
<th>No. collected</th>
<th>Sites (present/sampled)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lymnaea caperata</em></td>
<td>48</td>
<td>4/12</td>
</tr>
<tr>
<td><em>Lymnaea elodes</em></td>
<td>271</td>
<td>10/12</td>
</tr>
<tr>
<td><em>Lymnaea stagnalis</em></td>
<td>99</td>
<td>5/12</td>
</tr>
<tr>
<td><strong>Overall</strong></td>
<td><strong>418</strong></td>
<td><strong>10/12</strong></td>
</tr>
</tbody>
</table>

Discussion

To my knowledge, this study represents the first report of *F. magna* in moose populations in North Dakota. However, because the historical data we reviewed were collected by previous investigators, they were subject to a degree of interpretation. First, I assumed that flukes collected by past investigators were actually *F. magna*, as this fluke has been recovered from moose in this region (Lankester 1974, Murray et al. 2006), and the only other large liver fluke in North America, *Fasciola hepatica*, has not been reported in this area (Pybus 2001). Second, I interpreted all signs suggestive of *F. magna* infection as actually being caused by this parasite, although this may not have always been the case, as signs may have been due to injury, bacterial infection or potentially *Echinococcus granulosis* cysts (Jones and Pybus 2001, Leighton 2001). As a result, the true prevalence of *F. magna* in moose in eastern North Dakota may have been lower than the 19.5 % estimated from check station records and necropsy reports. Nonetheless, *F. magna* appears to be enzootic in moose in eastern North Dakota, although at a much lower prevalence than among moose in nearby northwestern Minnesota. For example,
Murray et al. (2007) reported an *F. magna* prevalence of 88% for moose in northwestern Minnesota in the late 1990s, while Karns (1972) reported 89% infection prevalence of *F. magna* among moose in the same region in the 1970s.

The failure to detect *F. magna* in 2002 and 2003 may have been due to the geographic distribution of my sampling. While the majority of historical reports of *F. magna* infection originated from Unit M1C (Figure 10), my ability to sample this area was limited because only ten moose tags/year were issued in this area in 2002 and 2003, compared to a total of 150 tags issued there from 1977-1984. Ultimately, only four of my samples from 2002-2003 were known to have originated from unit M1C (Table 7).

Importantly, however, my recent data confirm that *F. magna* is not highly prevalent in North Dakota moose and suggest that *F. magna* has not experienced a marked increase in prevalence since prior surveys were conducted. For example, based on binomial probability, I would have had a 95% chance of detecting *F. magna* in Unit M1C if the current prevalence was at least 60% and a 90% chance if the current prevalence was at least 53%. Also, given my sample size of 24 moose in the three units where historical data suggests *F. magna* occurs (M1C, M6, M8), I would have had a 95% probability of detecting this parasite even if it occurred at a moderate prevalence (14%). In addition, all of the 22 samples from unknown locations were also negative for signs of *F. magna* infection, and it is probable that a substantial proportion of these samples originated from the eastern part of the state. Therefore, *F. magna* likely infects a relatively small proportion of moose in eastern North Dakota. Additionally, the 2002-2003 provided a more complete sampling of the western part of the range of moose in the state (M4, M9,
M10; N=31), and results suggest that prevalence of *F. magna* is low in these areas as well.

Although my surveys for Lymnaeid snails were by no means exhaustive, I was able to collect Lymnaeid snails at ten of the 12 sites sampled. These results indicate that at least three species of suitable intermediate hosts for *F. magna* are widespread within the primary range of moose in the state. Natural or experimental infections of *L. caperata* and *L. stagnalis* have been observed (Foreyt and Todd 1978, Lausen and Stromberg 1993). While *L. elodes* has not been specifically identified as an intermediate host, *L. palustris* has been (Foreyt and Todd 1978, Laursen et al. 1989), and these two species are synonymous (Clarke 1973, and Hubendick 1951). The failure to recognize this synonymy in previous literature (Dunkel et al. 1996) has resulted in the exclusion of *L. elodes* as a potential intermediate host for *F. magna*.

Even though at least three species of intermediate hosts for *F. magna* appear relatively widespread in North Dakota, the extent to which their presence contributes to *F. magna* transmission to moose may be limited by persistence of seasonal wetlands. The range of moose in central and northeentral North Dakota (hunting units M4, M8, M9, and M10) lies within the larger “Prairie Pothole” region of the Great Plains (U. S. Fish and Wildlife Service 1955b). Wetlands are abundant in the Prairie Pothole region of North Dakota, but these habitats are subject to seasonal dry down and long-term drought cycles (Todhunter and Rundquist 2004, U.S. Environmental Protection Agency 1996, U. S. Fish and Wildlife Service 1955b). Thus on a seasonal or annual basis, environmental conditions may limit availability of intermediate hosts or aquatic vegetation, prevent
embryonation and hatching of eggs, and reduce survival of metacercaria (Pybus 1992, Swales 1935).

My data indicate that a large part of the primary range of *F. magna* in moose in North Dakota (Units M1C, M5, and M6) is within the northern Red River Valley, which is part of the Lake Agassiz Plain Ecoregion (U.S. Environmental Protection Agency 1996). Compared to the prairie pothole region of central and northcentral North Dakota, the Red River Valley has relatively few pond or small lake type wetlands. However, this area does include a number of permanent rivers and streams associated with the Red River. Riparian habitats associated with rivers and streams have been demonstrated to support *F. magna* transmission (Dunkel et al. 1996, Mulvey et al. 1991), and the Red River and its tributaries are known to support Lymnaeid snails (Clarke 1973, Cvancara 1983). Thus, I hypothesize that these habitats likely play the major role in transmission of liver fluke in moose populations in eastern North Dakota. While these riparian habitats make up a relatively small proportion of the overall landscape and may not be capable of sustaining high levels of *F. magna* infection, they may provide a more stable source of transmission than prairie pothole wetlands, allowing *F. magna* to persist at a moderate prevalence in this area.

While habitats capable of supporting *F. magna* transmission may not constitute a large proportion of the North Dakota landscape, this is not the case for much of northwestern Minnesota. While the Lake Agassiz Plain ecoregion extends into northwestern Minnesota, and includes a portion of the area where *F. magna* is enzootic among moose in Minnesota (Kams 1972, Murray et al. 2007, U.S. Fish and Wildlife Service 1955a, U.S. Fish and Wildlife Service 1955b), much of the Murray et al. (2007)
study area was within the Northern Minnesota Wetlands ecoregion (Figure 8). In contrast
to the Lake Agassiz Plain ecoregion, the Northern Minnesota Wetlands ecoregion is
characterized by a high proportion of standing water and permanent wetlands (Murray et
al. 2007, U.S. Environmental Protection Agency 1996). In addition, parts of the
Minnesota study that were located in the Lake Agassiz Plain ecoregion were areas with
abundant wetlands. For example, the Lake Agassiz National Wildlife Refuge (Figure 8)
is composed of 66% wetland and open-water habitats (Murray et al. 2007). Thus, the
higher *F. magna* infection prevalence observed in northwestern Minnesota compared to
that in eastern North Dakota is most likely due to differences between these two areas in
the availability of wetland habitats.

Although conditions in eastern North Dakota may support a moderate level of *F.
magna* transmission, whether infection prevalence in moose is high enough to make this
parasite a major source of mortality is questionable. The historical data reviewed in this
study were collected during a period of moose population growth, and *F. magna* infection
prevalence does not appear to have increased since that time. In fact, since the
completion of the current study, there has been only one report of an *F. magna* infected
moose in North Dakota, a sick adult cow moose collected from unit M6 (North Dakota
Game and Fish Department, unpublished data 2004). In addition, while only 18.8% of
moose necropsied as part of targeted surveillance showed signs of *F. magna* infection,
75.0% were infected with *P. tenuis*, suggesting that other mortality factors may be more
important than *F. magna*.

However, while *F. magna* may not be the direct cause of moose declines in
eastern North Dakota, this parasite appears to be endemic to the state, and it may be only
one of several factors combining to influence the health of the moose population. For example, although Murray et al. (2007) concluded that *F. magna* was the major source of mortality and morbidity in the declining moose population in northwestern Minnesota, prevalence of *F. magna* had not increased since the pre-decline period (Karns 1972), and they postulated that other factors, such as climate change and malnutrition, may have combined with *F. magna* to contribute to the collapse of the moose population in their study area. As a result, future investigations in North Dakota should consider how *F. magna* may interact with other stressors or pathogens such as the widespread and prevalent parasite *P. tenuis* or climate to affect moose population dynamics.
CHAPTER IV

DISTRIBUTION OF INTERMEDIATE HOSTS AND LANDSCAPE LEVEL FACTORS INFLUENCING PREVALENCE OF MENINGEAL WORM (PARELAPHOSTRONGYLUS TENUIS) INFECTION IN WHITE-TAILED DEER IN NORTH DAKOTA

Introduction

The transmission and geographic distribution of parasitic diseases are determined by spatially variable environmental factors that influence pathogen survival and the availability of intermediate and definitive hosts (Allan et al. 2003, Langlois et al. 2001, Ostfeld et al 2005). Changes in these environmental factors can alter transmission dynamics, thereby affecting the prevalence and distribution of disease (Collinge et. al 2005, Farnsworth et al. 2005, Glass et al. 2002, Hess et al 2002). Therefore, when studying the distribution of parasitic diseases it is important to consider how spatially variable elements such as climate, landscape structure, and host density may influence parasite transmission.

Parelaphostrongylus tenuis, the meningeal worm, is a nematode parasite that occurs in the dura mater, subdural space, and venous sinuses of the cranium of white-tailed deer (Odocoileus virginianus) (Anderson and Prestwood 1981). P. tenuis has an indirect life cycle requiring one of several species of terrestrial gastropod as intermediate hosts (Lankester 2001). Adult worms reside in the subdural space or venous sinuses of the craniums of white-tailed deer. First-stage larvae are shed in the feces of deer, and
gastropods become infected when feeding on fresh feces or when contacting larvae that have been washed on to litter or vegetation (Lankester 2001). *P. tenuis* can cause fatal neurological disease in several species of accidental host, including moose (*Alces alces*), elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) but its life cycle can generally only be completed in white-tailed deer (Anderson and Prestwood 1981).

Because of the requirements of the life-cycle of *P. tenuis*, the transmission potential of a given area depends on environmental factors that influence the distribution of definitive and intermediate hosts and affect the survival of first-stage larvae (Forrester and Lankester 1998, Lankester 2001, Shostak and Samuel 1984). For example, although *P. tenuis* is widely distributed in eastern North America, it is not found west of the mixed-grass prairies of the Great Plains, where relatively dry environmental conditions likely limit survival of gastropod intermediate hosts and the first-stage larvae of *P. tenuis* (Anderson 1972, Lankester 2001, Samuel and Holmes 1974). Also, white-tailed deer populations were historically uncommon in the Great Plains (Knue 1991), which is thought to be a second factor limiting the range of this parasite in the past (Bindernagel and Anderson 1972). However, hypotheses related to factors limiting the westward extent of *P. tenuis* have received little rigorous testing (Lankester 2001, Wasel et al 2003).

North Dakota is located at the western edge of the range of *P. tenuis* (Wasel et al 2003). However, native prairie habitats in the Great Plains and in North Dakota were greatly modified after European settlement by conversion to agriculture and widespread planting of tree rows/shelter belts to reduce wind erosion following the Dust Bowl years of the 1930s (Knue 1991, Licht 1997). Related to these changes white-tailed deer have
increased in abundance and expanded their range across much of North Dakota (Knue 1991, Smith et al. 2007). If these altered habitats also support intermediate hosts and permit the survival of first-stage larvae in the otherwise dry, open prairie, this habitat change may have also facilitated the range expansion of *P. tenuis*.

![Graph showing annual North Dakota firearm white-tailed deer harvest since 1991](image)

**Figure 11.** Annual North Dakota firearm white-tailed deer harvest since 1991 illustrating the increase in white-tailed deer abundance during this period.

In addition, while a previous survey for *P. tenuis* in North Dakota during the period 1989 to 1991, reported that 2 to 26% of white-tailed deer in the eastern half of North Dakota were infected with *P. tenuis* (Wasel 1995, Wasel et al. 2003), transmission conditions may have changed considerably since that time due to increased density of white-tailed deer (Jensen 2007, Smith et al 2007; Figure 11) and a recent long-term wet climate cycle beginning around 1993 (Todhunter and Rundquist 2004). *P. tenuis* has long been a management concern where moose and white-tailed deer are sympatric.
(Lankester 2001), and several moose in North Dakota exhibiting signs of infection have been observed (Lankester 2001) (North Dakota Game and Fish Department 1993). If *P. tenuis* increases in prevalence in eastern North Dakota, then the risk of infection to moose in the state may increase. Additionally, a westward expansion by this parasite will result in greater exposure to elk and mule deer that are also accidental hosts for the parasite. For these reasons a re-examination of this parasite in North Dakota was warranted.

My specific objectives in this study were to (1) estimate the infection prevalence of *P. tenuis* in white-tailed deer in North Dakota, (2) determine the extent of the distribution of this parasite within the state, (3) examine whether *P. tenuis* has recently increased its geographic range or infection prevalence within the state, (4) investigate how habitat directly contributes to transmission by harboring intermediate hosts, and (5) estimate the relative importance of white-tailed deer density, climate, and land cover for transmission of *P. tenuis* along the western margin of the range of the species.

**Methods**

*P. tenuis in White-Tailed Deer*

The prevalence of *P. tenuis* in white-tailed deer throughout North Dakota from 2002 to 2005 was estimated by examining deer heads collected from hunter check stations, meat locker plants, and by the North Dakota Game and Fish Department. Deer heads were cut sagitally using a butcher's band saw, and the cavernous, intercavernous, transverse, and sagittal blood sinuses; surface of the brain; and inner surface of dura mater of each head were examined for adult *P. tenuis* (Comer et al. 1991, Prestwood and Smith 1969). Deer were aged from tooth wear and eruption (Severinghaus 1949) and sex determined from presence or absence of antlers or antler pedicels. Infection status and.
Deer Management Unit (DMU; Figure 12) of origin was recorded for all deer examined. A statewide estimate of prevalence of *P. tenuis* infection in white tailed deer (no. infected/no. sampled) was determined as well as prevalence estimates for each of the 38 DMUs in North Dakota. Because the most detailed location data available for harvested deer was at the level of the DMU, all analyses were limited to this spatial resolution.

*Temporal Changes in Geographic Range and Prevalence*

I used meta-analyses to assess whether the geographic range and infection prevalence of *P. tenuis* in white-tailed deer in North Dakota increased between 1989-1991 and 2002-2005. Meta-analysis is a technique that is commonly used in literature reviews to combine the results of statistical tests from several studies into a single result. In the current study, relatively small sample sizes for many individual DMUs made it difficult to detect whether *P. tenuis* prevalence had changed in these units since the 1989-1991 survey. However, it was inappropriate to pool all DMUs together and conduct one comparison because of sample-size differences between DMUs. Meta-analysis allowed me to combine the results of separate comparisons for each DMU and identify any temporal changes in *P. tenuis* occurrence.

Based on the results of Wasel (1995), each DMU was designated as either a peripheral-range DMU or an established-range DMU. Peripheral-range DMUs were those where (1) *P. tenuis* was absent in 1989-1991 but present in 2002-2005, or (2) DMUs where *P. tenuis* was present in 1989-1991 but the DMU was spatially isolated from other DMUs with *P. tenuis*. Established-range DMUs were those where *P. tenuis*
was present in both 1989-1991 and 2002-2005, or DMUs that were entirely surrounded by DMUs with \textit{P. tenuis} during 1989-1991.

The relatively limited sampling of deer in 1989-91 may have failed to detect \textit{P. tenuis} in some DMUs when the parasite was actually present. Thus, the detection of \textit{P. tenuis} in these DMUs in the 2002-2005 survey would have suggested greater range expansion than actually occurred. To determine the probability that new occurrences of \textit{P. tenuis} in 2002-2005 represented recent range expansion by the parasite, I used one-tailed Fisher’s exact tests comparing the 1989-1991 and 2002-2005 data for each peripheral-range DMU. I then calculated a combined probability for all peripheral-range DMUs using: $P_{\text{combined}} = -2\Sigma \ln(P)$, where $P$ equals the probability of each individual test (Quinn and Keough 2002). To examine whether prevalence had increased in areas where the parasite was already established, these steps were repeated for established-range DMUs. I also conducted a random effects meta-analysis for established-range DMUs using the Rmeta package in R 2.6 (R Core Development Team 2007). This produced odds ratios for the increase in \textit{P. tenuis} prevalence for each DMU and an overall odds ratio for the entire established range. Additionally, I evaluated the possibility that any observed increase in prevalence in established-range DMUs was due to the lower proportion of fawns in the 2002-2005 sample (9%) compared to the 1989-1991 sample (24%). For this test I calculated the infection prevalence of all fawns (11% prevalence) and all $\geq$ one-year old deer (21% prevalence) sampled from established-range DMUs during 2002-2005 and created an adjusted 2002-2005 prevalence estimate based on a sample containing 24% fawns. A one-tailed Fisher’s exact test was used to compare this adjusted estimate to the 1989-1991 established-range estimate.
Model Selection

I constructed simple linear and multiple regression models and used model selection procedures to examine the influence of white-tailed deer density, climate, and land cover on transmission dynamics of *P. tenuis* in North Dakota. For all models, the arcsine-transformed estimate of *P. tenuis* prevalence (from the 2002-2005 survey) was used as the dependent variable with each DMU considered an observation. To ensure that estimates of *P. tenuis* prevalence were not biased by sampling intensity, I restricted analyses to the subset of 30 DMUs for which *P. tenuis* prevalence estimates were based on examination of at least 20 deer. All independent variables included in multiple regression models were standardized as necessary, or transformed to improve normality or reduce leverage of extreme values. Models were reduced using backward stepwise selection where the variable with the highest P-value was removed until only significant (α=0.05) variables remained, or only one variable remained in the model. The simple linear and reduced regression models were compared and ranked using Akaike’s Information Criterion for small sample sizes (AICc) (Burnham and Anderson 2002). All statistical analyses were performed in R 2.6 (R Development Core Team 2007).

Deer Density Model

If the westward limit of *P. tenuis* was influenced by the availability of white-tailed deer as definitive hosts, then I hypothesized that prevalence of *P. tenuis* would increase as abundance of white-tailed deer increased. I tested this hypothesis by assessing the fit of a simple linear regression model to data on prevalence of *P. tenuis* (dependent variable) and an index to deer abundance in each DMU in North Dakota. The index to deer abundance was the number of white-tailed deer harvested in each DMU.
during the 2001-2005 North Dakota firearm deer seasons (Jensen 2007; North Dakota Game and Fish Department) divided by size (km$^2$) of each DMU. I used deer harvest as an index to abundance because while reliable estimates of actual deer population density (deer/km$^2$) were not available, the number of deer tags issued per DMU was based on surveys of deer population trends, with more tags issued for units with greater deer abundance. Thus, harvest should be a reasonable reflection of deer population density.

Climate Models

I hypothesized that seasonal temperature and precipitation would influence the range and transmission potential for *P. tenuis* based on the influence of these abiotic factors on gastropod distribution and larval survival (Bickel 1977, Wasel et al. 2003). I anticipated that prevalence of *P. tenuis* would be higher in DMUs with relatively cool growing seasons and higher winter precipitation. These predictions were based on evidence that wetter habitat conditions promote increased abundance of gastropod intermediate hosts by the positive influence of moisture and relatively cool conditions on survival of first-stage larvae (Lankester and Anderson 1968, Shostak and Samuel 1984). I also hypothesized that prevalence would be negatively correlated with winter temperature because colder areas would experience fewer freeze-thaw cycles which negatively impact over-winter survival of larvae of *P. tenuis* and gastropod hosts (Forrester and Lankester 1998).

I obtained data on precipitation and temperature from 160 weather stations in North Dakota for the period 1963 to 2005 (National Climate Data Center; www.ncdc.noaa.gov); weather stations were mapped to DMUs, and data from all stations within individual DMUs were combined for estimating winter (Nov-April) and growing-
season (May-October) precipitation (cm), and mean temperature (°C) for each DMU. I chose the 1963-2005 interval to provide data for a relatively long time span (30 years) leading up to the beginning of the wet cycle in 1993. Climate data were then divided into three intervals, study period (2001-2005), wet cycle (1993-2005), historic (1963-1992), and I constructed a multiple regression model for each interval with growing-season temperature (GrTemp), winter temperature (WinTemp), growing-season precipitation (GrPrecip), and winter precipitation (WinPrecip) as independent variables, and *P. tenuis* prevalence as the dependent variable.

**Land Cover Models**

Woodland habitats may play a critical role in transmission by providing habitat for both intermediate and definitive hosts for *P. tenuis* (Kearney and Gilbert 1978, Lankester and Anderson 1968, Raskevitz et al. 1991, Smith et al. 2007). Also, in prairie-dominated regions of the northern Great Plains the wet meadow zone around semi-permanent and permanent wetlands may provide quality habitat for gastropod intermediate hosts (Jacques 2001, Oates 1999). Finally, although they do not appear to harbor gastropods, croplands near woodlands provide key foraging habitats for the definitive host for *P. tenuis* (Smith et al 2007, Cote et al. 2004). I therefore predicted *P. tenuis* prevalence would be positively related to the percent cover of woodland, wetland, cropland, and cropland spatially associated with woodland in North Dakota. These hypotheses were examined with a multiple regression model that included the percent cover of woodlands (%Wood), wetlands (%Wet), croplands (%Crop), and the interaction terms for woodlands and croplands (%Wood:Crop) and wetlands and croplands (%Wet:Crop).
Size and degree of isolation of habitats are closely linked to species richness (Lomolino and Weiser 2001), and may contribute to *P. tenuis* transmission by larger areas of woodlands or wetlands supporting abundant and more diverse assemblages of gastropod intermediate hosts. I therefore expected that DMUs with a larger mean patch size of habitats that contribute directly to transmission (woodlands and wetlands) would have greater *P. tenuis* prevalence compared to large areas of habitats not contributing to *P. tenuis* transmission (large expanses of grasslands and croplands). To test these hypotheses, I constructed a multiple regression model with mean patch size (m$^2$) of woodland (WoodPatch), wetland (WetPatch), cropland (CropPatch), prairie (PrairiePatch), and tame grass (TamePatch) habitats as independent variables as well as the interaction terms of woodland and cropland patch size (Wood:Crop) and wetland and cropland patch size (Wet:Crop). Similarly, I expected that DMUs with woodland or wetland patches that were more isolated from each other would be less capable of supporting *P. tenuis* transmission than those where woodlands or wetland patches were less separated. I tested this hypothesis with a multiple regression analysis that included the mean nearest-neighbor distance of woodland (NNwood) and wetland (NNwet) patches as independent variables.

Land cover data for modeling were acquired from the North Dakota Gap Analysis Project (United States Geological Survey 2005) and converted to vector form using the Spatial Analyst Extension in ArcGIS 9.2 (ESRI Inc, Redlands, CA, USA). Land cover types were collapsed into 5 major classes [woodland (all artificial and natural woodlands), cropland, tame grass, prairie, and wetland (semi-permanent wetlands, lakes, and rivers)] and clipped to the boundaries of each DMU. Percent cover for each habitat
type was determined by dividing the area of each cover type present in each DMU by the
area of the DMU. Mean patch area and mean nearest-neighbor distance within each DMU
were calculated using the Spatial Statistics Tool in ArcGIS 9.2.

Terrestrial Gastropods

To further investigate the potential of habitat to directly contribute to \textit{P. tenuis}
transmission, I sampled terrestrial gastropods in seven general habitat types at ten sites
throughout eastern North Dakota from 2003-2005 (Figure 12). Four sites were sampled
in 2003, and sampling was expanded in 2004 to include eight sites. Sampling in 2005
also included eight sites, which included six of the previously surveyed sites as well as
two new sites. Habitat types were defined as native prairie, tame grass (tame grasses,
alalfa, or old fields), tree row (planted tree rows one tree wide containing no leaf litter),
planted woodlot (planted tree rows or woodlots at least 2 trees wide containing leaf
litter/woody debris), woodland (naturally occurring woodlands), wet woodland (naturally
wooded riparian areas, lake or beaver pond edges), and row crop (sampled in 2003 only).

Gastropods were collected using cardboard coverboard transects. Each transect
consisted of ten 30 x 30 cm cardboard squares placed every 5m along each transect (Boag
1982). Squares were wetted, covered with clear plastic sheeting, and staked to the
ground to prevent displacement by wind (Lankester and Peterson 1996). After 48 hours,
each transect was checked. Collections took place in the morning before hot
temperatures and direct sunlight might have driven gastropods from coverboards. All
gastropods adhering to coverboards were collected, and stored in plastic containers lined
with moist paper towels until delivery to the laboratory for identification to species using
the criteria of Bickel (1977) and Burch (1962). In summer 2003, five transects were
placed in each habitat type at each site, and sites were sampled every two weeks. In 2004 and 2005 I accommodated sampling a larger number of sites by including three instead of five replicates in each habitat type and sampling every four weeks.

![Figure 12. Locations of ten terrestrial gastropod collection sites in North Dakota sampled during summers 2003, 2004, and 2005. Deer management units (DMU) are also indicated.](image)

I hypothesized that gastropods would be more abundant for transects in naturally occurring woodlands (woodlands and wet woodlands) than in other habitats. However, if planted woodlands (woodlots and tree rows) provide suitable habitat for gastropod hosts, then gastropod abundances in these habitats would be greater than in grassland habitats (native and tame grasslands). Abundance of gastropods was standardized for each transect by dividing the total number of gastropods collected by the number of times the transect was sampled. I used a series of planned contrasts with Wilcoxon rank sum tests to assess patterns in gastropod abundance for woodland compared to all other habitats,
for planted woodlots vs. grasslands, and for tree rows vs. grasslands. Preliminary results from gastropod sampling in 2003 suggested row crops had very limited potential to harbor gastropods, and this habitat type was not included in analyses.

Microclimate

Following the initial season of gastropod collection, I hypothesized that habitat types harboring greater numbers of gastropods would be relatively cool and moist (high relative humidity) compared to habitats harboring fewer or no gastropods. I assessed this hypothesis by taking hourly measurements of temperature and relative humidity with automatic weather recorders (Hobo data loggers; Onset Computer Corporation, Bourne, MA, USA) placed near the center point of all coverboard transects during summers 2004 and 2005. Weather recorders were mounted 4-5 cm above ground level inside inverted plastic sandwich containers (Rubbermaid Corporation, Atlanta, GA, USA). Data on mean daily maximum and mean daily minimum temperature and relative humidity were compiled and compared among habitats using repeated measures ANOVAs and Tukey’s post hoc tests.

Results

P. tenuis in White-Tailed Deer

A total of 3730 white-tailed deer originating from every Deer Management Unit in North Dakota were examined for presence of P. tenuis. P. tenuis was detected in 26 of the 38 DMUs, including 15 DMUs where it had not been reported previously. Overall prevalence of infection was 14.5% (95% C.I.=13.3-15.6%), but higher prevalences were apparent for DMUs in eastern North Dakota (Figure 13). Infection prevalence ranged from 0.7% in DMU 3A3 to 35.1% in DMU 2A. Notably, I detected P. tenuis infection in
two deer from DMUs 3B2 and 3E2 west of the Missouri River. *P. tenuis* was previously unknown for areas this far west in North Dakota (Figure 13).

![Figure 13. Map of the estimated infection prevalence of *Parelaphostrongylus tenuis* in North Dakota based on the examination of 3730 white-tailed deer from 2002-2005.](image)

Table 9. Results of meta-analysis comparing 1989-1991 and 2002-2005 estimates of *P. tenuis* prevalence in peripheral-range DMUs

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<td>920</td>
</tr>
</tbody>
</table>
Table 10. Results of meta-analysis comparing 1989-1991 and 2002-2005 estimates of *P. tenuis* prevalence in established-range DMUs

<table>
<thead>
<tr>
<th>Unit</th>
<th>1989-1991</th>
<th>2002-2005</th>
<th>P</th>
<th>Odds Ratio</th>
<th>95% C.I.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. Examined</td>
<td>Prevalence</td>
<td>No. Examined</td>
<td>Prevalence</td>
<td></td>
</tr>
<tr>
<td>2A</td>
<td>20</td>
<td>20.0%</td>
<td>37</td>
<td>35.1%</td>
<td>0.19</td>
</tr>
<tr>
<td>2B</td>
<td>23</td>
<td>17.4%</td>
<td>601</td>
<td>21.6%</td>
<td>0.43</td>
</tr>
<tr>
<td>2C</td>
<td>31</td>
<td>25.8%</td>
<td>146</td>
<td>30.8%</td>
<td>0.38</td>
</tr>
<tr>
<td>2D</td>
<td>25</td>
<td>24.0%</td>
<td>54</td>
<td>31.5%</td>
<td>0.34</td>
</tr>
<tr>
<td>2E</td>
<td>53</td>
<td>5.7%</td>
<td>186</td>
<td>12.4%</td>
<td>0.11</td>
</tr>
<tr>
<td>2F1</td>
<td>34</td>
<td>11.8%</td>
<td>227</td>
<td>22.5%</td>
<td>0.09</td>
</tr>
<tr>
<td>2F2</td>
<td>9</td>
<td>11.1%</td>
<td>181</td>
<td>21.0%</td>
<td>0.41</td>
</tr>
<tr>
<td>2G</td>
<td>6</td>
<td>16.7%</td>
<td>80</td>
<td>30.0%</td>
<td>0.43</td>
</tr>
<tr>
<td>2G1</td>
<td>22</td>
<td>13.6%</td>
<td>209</td>
<td>25.8%</td>
<td>0.15</td>
</tr>
<tr>
<td>2G2</td>
<td>33</td>
<td>12.1%</td>
<td>117</td>
<td>14.5%</td>
<td>0.49</td>
</tr>
<tr>
<td>2K2</td>
<td>55</td>
<td>1.8%</td>
<td>184</td>
<td>5.4%</td>
<td>0.23</td>
</tr>
<tr>
<td>2L</td>
<td>11</td>
<td>0.0%</td>
<td>58</td>
<td>31.0%</td>
<td>0.03</td>
</tr>
<tr>
<td>Total</td>
<td>322</td>
<td>12.0%</td>
<td>2080</td>
<td>21.2%</td>
<td>0.05</td>
</tr>
</tbody>
</table>

*Calculation of the overall odds ratio excludes DMU 2L

**Temporal Changes in Range and Prevalence**

With the possible exception of DMU 3A4 (P=0.08), results of meta-analyses suggest there was limited expansion by *P. tenuis* in North Dakota between the early 1990s and 2002 to 2005 (P=0.81; Table 9). However, results suggested *P. tenuis* infection increased within the established range DMUs between time periods (P=0.05, O.R.=1.7, 95% C.I.,1.2-2.5; Table 10). Increased prevalence was not the result of the lower proportion of fawns sampled during 2002-2005 (P<0.001).

**Model Selection**

Among six models identified as useful (α=0.05) for understanding variation infection prevalence of *P. tenuis* among white-tailed deer in North Dakota (Table 11, Figure 14), the highest ranked model was the wet-cycle climate model, which included
GrPrecip, WinTemp and GrTemp as significant terms (AIC = -55.6; Table 11). However, the second (historic climate, AIC = -42.0) and third (study-period climate, AIC = -33.0) included GrTemp as the single predictor variable. The percent cover model (%Wood, %Crop, %Wood:Crop; AICc = -23.5) was ranked next highest, followed by the deer density model (Deer/km²; AICc = -17.8), patch size model (WoodPatch, CropPatch, Wood:Crop; AICc = -16.0), and nearest-neighbor model (NNwood; AICc = -5.0).

Table 11. Results of model selection and summary of the reduced regression models constructed to examine the influence of climate, habitat, and white-tailed deer density on *P. tenuis* prevalence.

<table>
<thead>
<tr>
<th>Model</th>
<th>Variable</th>
<th>β</th>
<th>Model r²</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet-cycle climate*</td>
<td>GrPrecip</td>
<td>0.14</td>
<td>0.84</td>
<td>-55.2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>WinTemp</td>
<td>-0.10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>GrTemp</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Historical climate*</td>
<td>GrPrecip</td>
<td>0.18</td>
<td>0.70</td>
<td>-42.0</td>
<td>13.2</td>
</tr>
<tr>
<td>Study period climate*</td>
<td>GrPrecip</td>
<td>0.16</td>
<td>0.59</td>
<td>-33.0</td>
<td>22.2</td>
</tr>
<tr>
<td>Percent cover*</td>
<td>% Wet</td>
<td>0.10</td>
<td>0.48</td>
<td>-23.5</td>
<td>31.7</td>
</tr>
<tr>
<td></td>
<td>%Crop</td>
<td>0.15</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>%Wood:Crop</td>
<td>0.09</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deer density*</td>
<td>Deer/km2</td>
<td>0.10</td>
<td>0.33</td>
<td>-17.8</td>
<td>37.4</td>
</tr>
<tr>
<td>Patch size*</td>
<td>WoodPatch</td>
<td>0.09</td>
<td>0.33</td>
<td>-16</td>
<td>39.2</td>
</tr>
<tr>
<td></td>
<td>CropPatch</td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wood:Crop</td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nearest neighbor</td>
<td>NNwood</td>
<td>0.02</td>
<td>0.03</td>
<td>-5.0</td>
<td>50.2</td>
</tr>
</tbody>
</table>

*Models were significant at α = 0.05
Figure 14. Arcsine-transformed prevalence (y-axis) in relation to (a) wet-cycle growing season precipitation, (b) deer density, (c) wet-cycle winter temperature, (d) wet-cycle growing season temperature, (e) arcsine-transformed % crop cover, (f) arcsine-transformed % wetland cover, (g) natural log-transformed woodland patch size, and (h) natural log-transformed crop patch size.
Terrestrial Gastropods

We collected a total of 2778 gastropods from nine of the ten sites sampled during the three-year study period. Among the 15 species detected at coverboard transects (13 snails, two slugs), nine were known intermediate host species for *P. tenuis* (Table 12). *Deroceras laeve* (a slug), was the most common and widespread gastropod encountered (detected at nine different sites). Gastropods were more abundant in woodlands than all other habitats (*W* = 162.5, *P* < 0.001), but they were no more common in planted woodlots (*W* = 61, *P* = 0.070) than in tree rows or grasslands (*W* = 159.5, *P* = 0.74; Figure 15).

Table 12. Abundance of terrestrial gastropod species and number of sites at which each species was collected based on the sampling of ten sites in eastern North Dakota from 2003-2005.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. collected</th>
<th>Sites</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Deroceras laeve</em></td>
<td>979</td>
<td>9/10</td>
</tr>
<tr>
<td><em>Succinea ovalis</em></td>
<td>575</td>
<td>8/10</td>
</tr>
<tr>
<td><em>Discus cronkhitei</em></td>
<td>376</td>
<td>4/10</td>
</tr>
<tr>
<td><em>Zonitoides arboreus</em></td>
<td>210</td>
<td>6/10</td>
</tr>
<tr>
<td><em>Succinea avara</em></td>
<td>184</td>
<td>5/10</td>
</tr>
<tr>
<td><em>Cochlicopa lubrica</em></td>
<td>114</td>
<td>5/10</td>
</tr>
<tr>
<td><em>Vitrina limpida</em></td>
<td>94</td>
<td>5/10</td>
</tr>
<tr>
<td><em>Strobilops labrynthica</em></td>
<td>66</td>
<td>3/10</td>
</tr>
<tr>
<td><em>Vallonia collisella</em></td>
<td>58</td>
<td>7/10</td>
</tr>
<tr>
<td><em>Retinella electrina</em></td>
<td>54</td>
<td>7/10</td>
</tr>
<tr>
<td><em>Punctum minitussum</em></td>
<td>33</td>
<td>5/10</td>
</tr>
<tr>
<td><em>Succinea retusa</em></td>
<td>18</td>
<td>3/10</td>
</tr>
<tr>
<td><em>Euconulus fulvus</em></td>
<td>12</td>
<td>4/10</td>
</tr>
<tr>
<td><em>Stenotrema stenotrema</em></td>
<td>3</td>
<td>2/10</td>
</tr>
<tr>
<td><em>Deroceras reticulatum</em></td>
<td>2</td>
<td>1/10</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>2778</strong></td>
<td><strong>9/10</strong></td>
</tr>
</tbody>
</table>

*Known intermediate hosts for *Parelaphostrongylus tenuis*
Figure 15. Median number of gastropods collected (±inter-quartile range) for (a) naturally occurring woodlands vs. all other habitats ($W=162.5, P<0.001$), (b) planted woodlots vs. grasslands ($W=162.5, P<0.001$), and (c) tree rows vs. grasslands ($W=159.5, P=0.74$).

**Microclimate**

Mean daily maximum temperatures were coolest in natural woodlands and warmest in native prairie and meadow habitats ($F_{4, 19}= 30.1, P<0.001$; Figure 16). Similarly, planted woodlots and natural woodlands and tree rows had the highest mean daily minimum humidity ($F_{4, 18}= 24.5, P<0.001$; Figure 16).
Figure 16. Comparison of (a) Mean (±S.D.) daily maximum temperature ($F_{4,19}= 30.1$, $P<0.001$) and (b) mean daily minimum humidity ($F_{4,18}= 24.5$, $P<0.001$) for natural woodlands (Wood), planted woodlands (Pwood), tree rows, native prairie, and tame grass habitats. Values grouped under the same letter did not differ based on Tukey’s post-hoc tests.

Discussion

While the highest *P. tenuis* infection prevalence measured in this study was 35% in southeastern North Dakota (DMU 2A), prevalence was less than 20% in 16 of the 26 DMUs in which this parasite was detected (Figure 13). Based on these results, *P. tenuis* appears to be less common in North Dakota than in eastern North America where prevalence ranged from 44% to 90% in Michigan, Maine, Minnesota, New York, and Ontario (Boppel 1998, Bogacyk et al. 1993, Garner and Porter 1991, Lankester 2001, Lankester and Anderson 1968, Lankester and Peterson 1996, Reichard 1999, Slomke et al. 1995). This suggests that the transmission potential of *P. tenuis* is lower in North Dakota than in the eastern part of the parasite’s range. However, despite the relatively low infection prevalence of *P. tenuis* observed in this study, the geographic range of *P. tenuis* in North Dakota is considerably more extensive than previously thought, encompassing all but the southwestern part of the state. In addition, while Jacques and Jenks (2004) hypothesized that the Missouri River was a barrier at the western boundary
of the range of *P. tenuis*, we detected infected deer in two DMUs west of the Missouri River (3B2 and 3E2; Figure 13), suggesting that the Missouri River does not represent a hard boundary to the spread of this parasite.

While I did recover *P. tenuis* from 15 DMUs where it had not previously been reported, this does not appear to represent a recent expansion in the geographic range of this parasite. Meta-analysis of peripheral-range DMUs suggests that *P. tenuis* was present in those areas but was not previously detected because no samples were available for the DMU (n = 4), or the sample size within the DMU was too small for detection (n = 11) related to low prevalence (<15%). The possible exception was DMU 3A4. Although not significant at the α = 0.05 level (P = 0.08), the comparison between 1989-1991 and 2002-2005 data suggested the possibility that *P. tenuis* may have expanded to this unit after 1989-1991 (Table 9). Importantly, however, my results indicate that infection prevalence of *P. tenuis* among white-tailed deer in DMUs in eastern North Dakota has increased significantly since the early 1990s. Multiple regression modeling supported this result and suggested increased prevalences of *P. tenuis* in white-tailed deer were the combined result of the long-term wet-cycle in eastern North Dakota after 1993 and increased abundance of white-tailed deer.

Modeling of parameters influencing *P. tenuis* infection indicated, that at the broad scale at which this study was conducted, climate was the most important determinant of the current geographic range and observed infection prevalence for *P. tenuis* in North Dakota. Current infection prevalence was most strongly related to climate since the beginning of the recent wet cycle in 1993. However, analyses also identified a strong correlation between historical climate (1963-1992) and current *P. tenuis* prevalence. I
interpret these results as indicating that the long-term climate regime is a primary
determinant of whether *P. tenuis* may occur in a given area, and as such, it would be
expected that infection prevalence would be correlated with historic climate. However,
within areas where the overall climate supports *P. tenuis* transmission, current infection
prevalence is directly related to the influence of shorter-term climate cycles on
transmission conditions. Results of meta-analyses support this idea, suggesting that
while *P. tenuis* prevalence has increased during the recent wet cycle, this parasite has not
expanded its geographic range beyond areas that have historically supported
transmission.

Of the climate variables examined, growing season precipitation appears to have
the strongest influence on *P. tenuis* transmission. For all three climate models, infection
prevalence was higher in areas with relatively high precipitation during the growing
season. Growing season precipitation may be important for *P. tenuis* larval survival by
maintaining a moist mucous coating on the outside of feces containing larvae (Shostak
and Samuel 1984). Precipitation also likely influences the abundance and availability of
terrestrial gastropods, because snails and slugs are more active and occur in greater
numbers in wetter areas (Bickel 1977, Burch 1962).

The final wet-cycle climate model identified two additional variables as also
influencing *P. tenuis* transmission. The positive relationship between mean growing
season temperature and *P. tenuis* prevalence in the wet-cycle model was the opposite of
my original prediction. As opposed to higher summer temperatures limiting larval
survival and gastropod availability, warmer average temperatures during spring and fall
may facilitate *P. tenuis* transmission by providing a longer period for gastropods
intermediate hosts to remain active. Further, I predicted that prevalence of *P. tenuis* would be higher when winters were colder, related to the negative association between number of freeze-thaw cycles and overwinter survival by larvae and gastropods (Forrester and Lankester 1998). This idea was supported by the wet-cycle climate model, which included a negative correlation between winter temperature and *P. tenuis* prevalence (Table 11).

Although abundance of deer was not included in any of the four top ranked models, the deer density model was significant and identified a positive relationship between the index to deer density and *P. tenuis* prevalence. This result was supported by habitat models, which indicated that factors that increased the availability of deer also resulted in higher *P. tenuis* prevalence. Thus, the historic conversion of prairie to agriculture and the proliferation of planted woodlands/shelterbelts after the 1930s may have facilitated the transmission of *P. tenuis* by providing habitat for deer. Also, the observed relationship between deer abundance and *P. tenuis* prevalence suggests that the recent increase in *P. tenuis* prevalence in eastern North Dakota may be in part due to the rise in white-tailed deer numbers in North Dakota since the 1990s (Knue 1991, Smith et al. 2007).

The percent cover and patch size models were ranked lower than climate models, ranking fourth and sixth, respectively, yet they still explained a significant amount of the variation in *P. tenuis* prevalence. As a result, habitat also appears to influence *P. tenuis* transmission in North Dakota. Contrary to my expectation, percent woodland cover (%Wood) was not an important predictor of *P. tenuis* prevalence, although the interaction term for woodland cover and crop cover was retained in the final percent cover model,
revealing that DMUs including wooded areas adjacent to croplands have higher prevalences of *P. tenuis* in their white-tailed deer. This result was reinforced by the model for habitat patch size, which indicated that DMUs with large blocks of woodland, large blocks of cropland, and large woodlands in association with large agricultural fields provide good conditions for *P. tenuis* (Table 11). I interpret evidence for positive relationships between percent cover and size of patches of croplands and woodlands as identifying key habitat components important for the definitive host of *P. tenuis*, white-tailed deer. Previous work has identified croplands in association with cover habitats (natural or planted woodlands) as providing high suitability habitats that support increasingly abundant white-tailed deer in North Dakota (Smith et al. 2007). Further, results from coverboard transects revealed that both abundance and diversity of gastropod intermediate hosts were highest in natural woodlands. Thus, the positive relationships identified in our model for *P. tenuis* prevalence and areas of croplands, croplands associated with woodlands, and larger patches of each can be interpreted as contributing to transmission by supporting abundant populations of both definitive and intermediate hosts for the parasite. Additionally, our finding that higher *P. tenuis* prevalence was associated with wetland cover supports the conclusions of Jacques (2001) and Oates (1999), suggesting that these areas may contribute to transmission of *P. tenuis* in North Dakota by harboring gastropod intermediate hosts.

The nearest-neighbor model was not significant at the $\alpha = 0.05$ level and ranked lowest for understanding infection prevalence of *P. tenuis* among North Dakota DMUs. The reduced model included a variable describing distance between patches of woodland habitats (NNWoodland). We suspect this result may be related to the relatively low
number of woodland patches in all DMUs and their tendency, when present, to possess a clumped distribution.

Gastropod sampling revealed that at least nine species of known gastropod intermediate hosts for *P. tenuis* are present in North Dakota. Among the species recovered, three of the most abundant (*D. laeve* and *D. cronkhitei*, and *Z. arboreus*) were identified as important intermediate hosts in other areas, and they likely fulfill the same role in North Dakota (Kearney and Gilbert 1977, Lankester and Anderson 1968, Lankester and Peterson 1996, Platt 1989). Results also indicated that natural woodlands are crucial for transmission of *P. tenuis* in North Dakota, as these habitats harbored the most abundant populations of snails and slugs. This provides an explanation for the positive relationship between prevalence and woodland patch size observed in land cover modeling, and agrees with studies in other regions (Boppel 1998, Kearney and Gilbert 1978, Lankester and Anderson 1968, Raskevitz et al. 1991). Lankester and Anderson (1968) suggested that deciduous woodlands support intermediate hosts by providing cool, moist conditions for snails and slugs, and analyses of data from temperature and humidity sensors placed along coverboard transects found this to be the case; natural woodlands were cooler and wetter than more open habitats. Importantly, however, although temperature and humidity in planted woodlots was very similar to natural woodlands, planted woodlots did not support abundant and diverse assemblages of snails and slugs. It is possible that the scarcity of gastropods in many of the planted woodlots we sampled was due to their location in central North Dakota where the overall climate is dryer than in eastern North Dakota where most of the natural woodlands we sampled were located. Previous surveys of gastropods in North Dakota were in accord with our results; Bickel
(1977) and Cvancara (1973) found relatively few gastropods in wooded habitats of western North Dakota compared to woodlands in the eastern third of the state.

One limitation of our study was a lack of information on intermediate host gastropods in wetland habitats. Other studies have reported presence of gastropod intermediate hosts for *P. tenuis* in wetland areas (Jacques 2001), which may explain the importance of wetlands in our models for *P. tenuis* (Table 11). We attempted to sample wetland edges for terrestrial gastropods in 2004 and 2005, but collection efforts were compromised when transects were repeatedly flooded by heavy summer rains. Future studies should attempt to sample for gastropods in wetland habitats.

In summary, this study has redefined the distribution of *P. tenuis* in North Dakota while demonstrating the combined importance of climate and habitat as determinants of infection rates for *P. tenuis* in white-tailed deer in the northern Great Plains. While habitat is important for transmission because of its influence on the abundance of both definitive and intermediate hosts, at the broad scale, the primary determinant of the distribution and prevalence of *P. tenuis* is climate. Specifically, the longer term background pattern of growing season precipitation has determined the geographic range of this parasite in North Dakota, while periodic climate cycles are the primary factors influencing infection prevalence. Therefore, while woodland and possibly wetland habitats are critical for *P. tenuis* transmission in eastern North Dakota where rainfall is plentiful during spring and summer, in the dryer central part of the state, these same habitats are less suitable for survival and maintenance of abundant gastropod intermediate hosts for *P. tenuis* and survival of the first-stage larvae of this parasite. As a result, activities that increase white-tailed deer density (agriculture), or create habitat for
snails and slugs (planting of woodlots and shelterbelts) may influence infection prevalence where the climate is favorable for transmission, but these activities appear unlikely to facilitate additional expansion by this parasite much beyond its current limit slightly west of the Missouri River. These results support the hypothesis that the Great Plains represent a barrier to the westward expansion of *P. tenuis* (Lankester 2001, Samuel and Holmes 1974) and are important for suggesting that this parasite will likely not pose a major threat to populations of mule deer, and elk in western North Dakota, even as white-tailed deer continue to increase and expand westward into the mixed and shortgrass prairies in North America. In contrast, based on my findings, the current range of *P. tenuis* completely encompasses that of the state’s moose population, including the area where infection prevalence in white-tailed deer has recently increased. As a result, *P. tenuis* remains a disease concern for moose in North Dakota, and the extent to which climate fluctuations, habitat alteration, and white-tailed deer density influence transmission risk to moose may have important implications for the moose population in the state.
CHAPTER V

MOOSE POPULATION TRENDS IN NORTH DAKOTA: THE POTENTIAL INFLUENCE OF CLIMATE, HARVEST, WHITE-TAILED DEER DENSITY, AND PARASITIC DISEASE INFECTION

Introduction

In the southern part of their range, declines in moose (Alces alces) populations have been attributed to human-induced habitat change, the recovery of large predator populations, overexploitation, or exposure to parasites of white-tailed deer (Aho and Hendrickson 1989, Lankester 2001, Lankester and Samuel 1998, Murray et al. 2006). Of these examples, perhaps the most well known is the purported effect of meningeal worm (Parelaphostrongylus tenuis) on moose populations where moose and white-tailed deer occur sympatrically (Gilbert 1973, Lankester 1974, Lankester and Samuel 1998). For several decades, researchers have considered P. tenuis to be a limiting factor for moose. However, while the effects of this parasite may be more subtle than initially believed, the size of moose populations has been correlated with P. tenuis prevalence in deer as well as deer density (Dumont and Crete 1996, Whitlaw and Lankester 1994, Gilbert 1973, Karns 1967). More recently, another parasite of white-tailed deer, the liver fluke (Fascioloides magna), has been identified as an important cause of moose mortality (Aho and Hendrickson 1989, Murray et al. 2006), further raising concerns over the effects of parasite-mediated competition between deer and moose (Murray et al. 2006).

Additionally, both climate cycles and climate change have recently been implicated in influencing the dynamics of moose populations (Murray et al. 2006, Post
and Stenseth 1998). In general, climatic processes can influence population dynamics directly by creating severe winter conditions, drought, or by causing thermal stress, all of which may result in higher mortality and lower fitness for ungulates. Climate changes may also indirectly affect populations by exacerbating the deleterious effects of parasitic disease or poor nutrition (Murray et al. 2006), facilitating the range expansion of competitors, or increasing the transmission of pathogens (Harvell et al. 2002, Jenkins et al. 2005, Purse et al. 2005, Thomas et al. 2004).

Following extirpation by European settlers, a resident moose population in North Dakota has become re-established since the 1960s, experiencing a long period of growth and expansion (Johnson 1992, Knue 1991). While the moose population appears to be doing well throughout most of its range in North Dakota, since 1996, aerial surveys conducted by the North Dakota Game and Fish Department have indicated a steady decline in the segment of the moose population present in the northeastern part of the state (Johnson 2007; Figure 9). Coincident with this decline has been an unprecedented increase in the range and abundance of white-tailed deer in the state (Knue 1991, Smith et al. 2007; Figure 11) as well as a similar long-term decline in the number of moose in adjacent northwestern Minnesota (Murray et al. 2006). Murray et al. (2006) attributed the decline of the moose population in northwestern Minnesota to the effects of climate warming acting in concert with parasitic diseases carried by white-tailed deer (primarily *F. magna* infection and to a lesser degree *P. tenuis*). In North Dakota, moose exhibiting signs of infection by *P. tenuis* have recently been reported, and *F. magna* has been recovered from hunter-killed moose in North Dakota in the past (North Dakota Game and Fish Department, unpublished data). As a result, concern exists that the decline in the
number of moose in northeastern North Dakota may be the result of the same processes that produced the Minnesota decline. For this project, I examined trends in moose populations in the three moose aerial survey areas in North Dakota and compared these trends to hunter harvest intensity, climate, white-tailed deer abundance, and parasitic disease risk. With this comparative approach, I hypothesize that differences in population trends for moose population trends among the three study sites should be accounted for by differences in one or more of these factors.

Methods

*Moose Population Estimates*

I examined moose population trends in North Dakota using data from annual winter aerial surveys conducted by the North Dakota Game and Fish Department from 1980-2006. Management of moose populations in North Dakota is divided into four moose management units (MMUs), Pembina Hills, Turtle Mountains, Drift Prairie, and Red River Valley (Figure 17), with dedicated moose aerial surveys carried out in survey areas located in three of the MMUs (Figure 17). The Pembina Hills aerial survey area in the northeastern corner of the state is a 750 km² area located along the Pembina Escarpment characterized by rolling topography and aspen (*Populus tremuloides*) woodlands associated with the Pembina and Tongue Rivers (North Dakota Forest Service 2003, Stevens 1966). The Turtle Mountains survey area is a 240 km² block in north-central North Dakota. This area is characterized by hilly woodlands of primarily aspen and bur oak (*Quercus macrocarpa*), numerous small lakes and wetlands, and interspersed agricultural land (Bakke 1980, North Dakota Forest Service 2003, Stevens 1966). The Drift Prairie monitoring block encompasses a 3030 km² area in the drift prairie region of
the state. This area is characterized by a gently rolling topography and numerous small wetlands characteristic of the prairie pothole region (Stevens 1966). Much of the land has been converted to agricultural use, and planted woodlots and tree rows are scattered across the landscape. Surveys were conducted with fixed-wing aircraft by flying linear transects at one-half mile intervals over each area. Surveys were conducted only in winters when snow depth was greater than 30 cm on the level (Johnson 2002).

Moose Harvest

I also investigated whether hunter harvest may have influenced moose population trends in North Dakota. Currently, North Dakota annually issues 100-175 once-in-a-lifetime tags by lottery, with the number of tags in each MMU determined primarily from winter aerial surveys and the input of local landowners (Johnson 2002). The North Dakota Game and Fish Department collects information from moose hunters to estimate the number of animals harvested, determine location of kills, and estimate the age/sex structure of moose harvest. However, because complete censuses of the moose population are not conducted, it was not possible to use harvest data to directly determine the proportion of the moose population taken annually by hunters. Instead I estimated harvest rate by determining how many moose were harvested in each MMU, and how many of those harvests occurred within the aerial survey units (where a winter count of moose was available). I first calculated the mean ratio of annual harvest: aerial survey count for each MMU (harvest:winter count). I then estimated the proportion of the overall harvest for each MMU that occurred within the aerial survey area as opposed to elsewhere in the MMU. This was determined by first mapping the locations of 1500 moose killed by hunters from 1977-2005 to Public Land Survey Township and Range (92
km² areas). Any moose harvested in townships having their centroid within an aerial survey area were then considered to have been harvested in the survey area (*survey area harvest*). The total number of moose harvested within an aerial survey unit was then divided by the total number of moose harvested in that MMU (*total harvest*). This proportion was multiplied by the mean harvest: winter count ratio, providing an estimate of the proportion of the count during the winter survey that was harvested. This can be expressed as:

\[
\text{Estimated harvest rate} = \frac{\text{survey area harvest}}{\text{total harvest}} \times \text{harvest: winter count}
\]

This serves as an estimate the average harvest rate for each MMU since the onset of moose seasons.

Figure 17. North Dakota moose management units (MMUs) and moose aerial survey areas.
Climate Trends

I obtained data on precipitation, temperature, dates of last and first annual freeze, and growing season length from seven weather stations located within or in close proximity to each moose survey area for the period 1965 to 2005 (National Climate Data Center; www.ncdc.noaa.gov). I hypothesized that moose population trends would be negatively correlated with warming temperatures, as reported by Murray et al. (2006) in northwestern Minnesota. In order to permit direct comparison with the Murray et al. (2006) study, mean temperature and total precipitation were combined into two-month intervals (January-February, March-April, May-June, July-August, September-October, November-December). Values were then averaged for the weather stations associated with each moose survey area. I used simple linear regressions to investigate trends in climate variables over time (year) for each of the three survey areas. All statistical analyses were performed in R 2.6 (R Development Core Team 2007).

In order to examine the relationship between moose population trends and climate trends, I compared all climate variables showing a significant trend (α ≤ 0.05) in simple linear regressions over the 1965-2005 period for any of the MMUs to moose population growth rate within each survey area. I accounted for autocorrelation between successive observations by applying a correction factor (df = N[(1 - a1a2)/(1 + a1a2)]) to the regression results, where N was the number of paired samples and a1 and a2 represent the level of first-order autocorrelation for the response and explanatory variables, respectively (Patterson and Powers 2002). Moose population growth was calculated as the annual rate of population change (ln[Nt+1/Nt]) (Murray et al. 2006). Although population estimates were available for most years, it was necessary to extrapolate
growth rates for years when surveys were not conducted because of insufficient snow cover. In these cases I estimated the moose count for missing years by averaging the counts for the years before and after the missing value and calculated a growth rate based on this count estimate. I then used simple regressions to examine whether annual growth rates of the moose population in each survey area were correlated with climate variables at a one-year time lag. While I recognize the potential for populations to be affected by variables at longer time lags, a one-year lag was chosen because this interval was the best predictor in the Murray et al. (2006) study. Additionally, preliminary modeling (simple linear regressions at two and three-year lags) indicated that any significant relationships present at two and three-year lags were also present at a one-year lag.

Moose Populations vs. White-Tailed Deer Abundance

I also compared moose population trends in the three survey areas with those of deer populations. I hypothesized that decreasing moose populations would occur where white-tailed deer populations were increasing, potentially as a result of parasite-mediated competition. An index to white-tailed deer abundance for each moose aerial survey area was created based on available deer harvest estimates (1980-2005) for the three deer management units in which the moose survey areas were located. This was calculated as the number of white-tailed deer harvested each year in each deer management unit during the North Dakota firearm deer seasons divided by size (km$^2$) of each DMU (Jensen 2007; W. F Jensen, North Dakota Game and Fish Department, unpublished data). I used deer harvest as an index to abundance because while reliable estimates of actual deer population density (deer/km$^2$) were not available for most of this period, the number of deer tags issued per DMU was based on surveys of deer population trends, with more
tags issued for units with greater deer abundance. Thus, harvest should be a reasonable reflection of deer population density, given that hunter success rates are consistent over time (Jensen 2007). Moose population growth rates for 1991-2006 were then regressed against the previous year’s deer abundance, with results adjusted for temporal autocorrelation, as described above.

Parasitic Disease Risk

For this project I chose to focus my investigation of parasitic disease risk on *P. tenuis*, because concurrent research had addressed the status of *F. magna* in North Dakota moose, concluding that this parasite was relatively rare in the state (Chapter 3). I hypothesized that risk of *P. tenuis* transmission would be higher in areas where moose were declining compared to areas where numbers were stable or increasing. From 2002-2005, I assessed the prevalence of *P. tenuis* infection in white-tailed deer for the 18 North Dakota deer management units (DMUs) occurring within moose range by examining intact deer heads collected from hunter check stations, meat locker plants, and by the North Dakota Game and Fish Department. Moose range was defined as all DMUs occurring within areas open to moose hunting or where moose populations were otherwise known to be established. Deer heads were cut sagitally using a butcher’s bandsaw, and the cavernous, intercavernous, transverse, and sagittal blood sinuses; surface of the brain; and inner surface of dura mater of each head were examined for adult *P. tenuis* (Comer et al.1991, Prestwood and Smith 1969). Infection status and DMU of origin was recorded for all deer examined.

I investigated the potential relationship of climate and white-tailed deer density to *P. tenuis* prevalence by constructing a series of simple linear models that used climate
parameters or deer-density as predictors of the arcsine-transformed estimate of *P. tenuis* prevalence. Climate data for 1993-2005 were obtained from 60 weather stations within the range of North Dakota moose. Weather stations were mapped to DMUs, and data from all stations within individual DMUs were combined to estimate climate parameters. Variables included in climate models were determined *a priori*, and included winter (Nov-April) and growing-season (May-October) precipitation (cm), mean temperature (°C) in the same two-month intervals used in prior analyses, and growing season length (days). The 1993-2005 interval was chosen because of the strong influence of a post-1993 wet cycle on observed climate trends (Figure 19). The deer-density predictor variable was the index to deer abundance for each moose-range DMU based on mean annual firearm harvest from 2001-2005 divided by DMU area (km²). Data from 2001-2005 were used because of the potential direct relationship to *P. tenuis* prevalence estimates from the 2002-2005 survey.

I then used the results of linear modeling to map the relative risk of *P. tenuis* infection throughout the range of moose in North Dakota. All models that were significant at the \( \alpha = 0.05 \) level were compared and ranked using Akaike’s Information Criterion for small sample sizes (AICc) and AIC weights (Burnham and Anderson 2002) to determine their relative importance in predicting *P. tenuis* prevalence. Climate variables from significant models were mapped by using ordinary kriging in ArcGIS Geostatistical Analyst (Environmental Systems Research Institute, Redlands, CA) to interpolate standardized climate data from the 60 weather stations. Deer density for each DMU was mapped as a raster dataset using the Spatial Analyst Extension in ArcGIS 9.2. I then used AIC weights from the linear models to produce a weighted-overlay that
combined climate and deer-density layers to create a map of relative *P. tenuis* infection risk.

The initial map was further modified to reflect infection risk based on the distribution of habitats that contribute directly to infection. Research has indicated that woodlands and potentially wetlands are critical to *P. tenuis* infection because these habitats harbor the gastropod intermediate hosts required to support the indirect life cycle of *P. tenuis* (Chapter 4; Boppel 1998, Jacques 2001, Kearney and Gilbert 1978, Lankester and Anderson 1968, Oates 1999, Raskevitz et al. 1991). Thus, even if climate and deer density influence infection risk at the broad scale, the presence of woodland and wetland habitats is still likely necessary for transmission to occur. Land cover data from the North Dakota Gap Analysis Project (United States Geological Survey 2005) were used to map all woodland and semi-permanent and permanent wetland habitats within North Dakota moose range. Woodland and wetland layers were then converted to vector form using the Spatial Analyst Extension in ArcGIS 9.2 and the risk map was clipped to the boundaries of these habitats with the Spatial Statistics Tool in ArcGIS 9.2. The result was a map estimating the relative risk of *P. tenuis* infection within habitats that have the potential to directly contribute to transmission. In order to evaluate this map, I then plotted locations of all 40 confirmed *P. tenuis*-related moose mortalities based on data collected by the North Dakota Game and Fish Department from 1982-1993 and 2006-2008.

**Results**

*Moose Population Trends*

Survey data showed disparate population trends for the three moose survey areas. Following a peak count of 260 animals in 1995, moose in the Pembina Hills experienced
a steady decline with only 11 animals observed in the 2006 survey (Figure 9). In contrast, in the Drift Prairie area, moose numbers have increased considerably since the first aerial survey in 1987. Although moose numbers in the Turtle Mountains have experienced considerable fluctuations over the years, an overall trend was not apparent (Figure 9).

Figure 18. Distribution of North Dakota moose harvest in relation to the three aerial survey units based on harvest locations of 1500 moose mapped to Public Land Survey Township and Range.

Moose Harvest

On average, the ratio of annual harvest: aerial survey count was 0.28 for the Pembina Hills MMU, 0.40 for the Turtle Mountains and 0.52 for the Drift Prairie, with a disproportionate number of harvest locations occurring within aerial survey areas compared to the rest of the area within MMUs. In the Pembina Hills, 91% of known harvest locations occurred within or in direct proximity to the aerial survey area, which encompasses approximately 13% of the Pembina Hills MMU (Figure 18). In the Turtle
Mountains, 42% of the known harvest locations were from within the aerial survey area, which comprises 18% of the Turtle Mountains MMU, while 48% of the harvest in the Drift Prairie MMU occurred within the aerial survey area, which makes up 9% of that MMU (Figure 18). Based on these data, 26.7% of Pembina Hills moose were harvested annually, while harvest rates for the Drift Prairie and Turtle Mountains were 25.0% and 16.8%, respectively.

Table 13. Change in climate variables in the Pembina Hills, Turtle Mountains, and Drift Prairie moose survey areas (1965-2005) based on results of simple linear regressions. Slope is represented by β.

<table>
<thead>
<tr>
<th></th>
<th>Pembina Hills</th>
<th></th>
<th>Turtle Mountains</th>
<th></th>
<th>Drift Prairie</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>β</td>
<td>R²</td>
<td>P</td>
<td>β</td>
<td>R²</td>
<td>P</td>
</tr>
<tr>
<td>Precipitation</td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>March-April</td>
<td>-0.034</td>
<td>0.052</td>
<td>0.082</td>
<td>-0.040</td>
<td>0.073</td>
<td>0.048</td>
</tr>
<tr>
<td>May-June</td>
<td>0.099</td>
<td>0.23</td>
<td>0.00093</td>
<td>0.083</td>
<td>0.13</td>
<td>0.012</td>
</tr>
<tr>
<td>Jul-August</td>
<td>-0.041</td>
<td>-0.025</td>
<td>0.93</td>
<td>-0.043</td>
<td>-0.019</td>
<td>0.61</td>
</tr>
<tr>
<td>Sept-Oct</td>
<td>-0.015</td>
<td>-0.014</td>
<td>0.52</td>
<td>-0.034</td>
<td>0.015</td>
<td>0.21</td>
</tr>
<tr>
<td>Nov-Dec</td>
<td>1.80</td>
<td>-0.010</td>
<td>0.45</td>
<td>0.78</td>
<td>-0.023</td>
<td>0.75</td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan-Feb</td>
<td>0.062</td>
<td>0.028</td>
<td>0.15</td>
<td>0.096</td>
<td>0.090</td>
<td>0.032</td>
</tr>
<tr>
<td>May-June</td>
<td>-0.071</td>
<td>0.41</td>
<td>&lt;0.0001</td>
<td>-0.073</td>
<td>0.40</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Jul-August</td>
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<td>0.075</td>
<td>0.045</td>
<td>-0.032</td>
<td>0.16</td>
<td>0.0056</td>
</tr>
<tr>
<td>Sept-Oct</td>
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<td>0.27</td>
<td>0.00033</td>
<td>-0.015</td>
<td>0.0096</td>
<td>0.25</td>
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<td>Growing Season</td>
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<td></td>
</tr>
<tr>
<td>Last freeze</td>
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<td>-0.083</td>
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<td>0.74</td>
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<td>First freeze</td>
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<td>0.098</td>
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<tr>
<td>Season length</td>
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<td>0.0027</td>
<td>0.41</td>
<td>0.039</td>
<td>0.18</td>
</tr>
</tbody>
</table>

Climate Trends

Over the 41-year time series, May-June precipitation was greater for all three survey areas, as was November-December precipitation in the Drift Prairie area (Table 13). In contrast, March-April precipitation decreased from 1965-2005 in the Turtle Mountains. July-August temperatures showed a cooling trend from 1965-2005 for all three survey areas, as did May-June temperatures for the Turtle Mountains and Pembina Hills, and September-October temperatures for the Pembina Hills (Table 13, Figure 19). January-February temperatures, however, were significantly warmer in the Turtle
Mountains over the 41-year time series, and the Pembina Hills and Cando areas demonstrated similar trends, although they were not significant at the $\alpha = 0.05$ level after adjusting for autocorrelation (Table 13). Additionally, despite cooler summer temperatures, the date of first freeze was actually later and the growing season was longer in the Pembina Hills and Cando areas (Table 13, Figure 19). The observed trends for wetter and cooler summer climate appear to be associated with a wet climate cycle that affected eastern North Dakota beginning in 1993 (Figure 19; Todhunter and Rundquist 2004).

**Figure 19.** Temporal change in May-June precipitation (a), growing season length (b), May-June temperature (c), and July-August temperature (d) for the Pembina Hills survey area in northeastern North Dakota (1965-2005).

**Moose Population vs. Climate and White-Tailed Deer Abundance**

Moose population growth rates in the Pembina Hills were negatively correlated with March-April and May-June precipitation, and were positively correlated with May-June and July-August temperature (Table 14). Growth rates in the Pembina Hills also
decreased with increasing growing season length and later date of first freeze (Table 14). Moose population growth rates in the Turtle Mountains and Drift Prairie areas showed no significant relationship to any of the climate factors investigated. Moose population growth rates were negatively correlated with the abundance of white-tailed deer in the Pembina Hills and Drift Prairie areas (Table 14, Figure 20). I detected no significant relationship between deer abundance and moose population growth the Turtle Mountains after results were adjusted for autocorrelation (Table 14, Figure 20).

Figure 20. Relationship of moose population growth rate to firearms-season white-tailed deer harvest density for the Pembina Hills, Turtle Mountains and Drift Prairie moose survey areas.
Table 14. Relationship of climate variables and white-tailed deer density to moose population change in the three North Dakota moose survey areas. Probabilities are for two-tailed t-tests adjusted for autocorrelation.

<table>
<thead>
<tr>
<th></th>
<th>Pembina Hills</th>
<th></th>
<th>Turtle Mountains</th>
<th></th>
<th>Drift Prairie</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>β</td>
<td>R²</td>
<td>P</td>
<td>β</td>
<td>R²</td>
<td>P</td>
</tr>
<tr>
<td>Precipitation</td>
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<td></td>
</tr>
<tr>
<td>May-June</td>
<td>-0.041</td>
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<td>-0.034</td>
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<td>March-April</td>
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<td>0.042</td>
<td>0.037</td>
<td>0.026</td>
<td>0.21</td>
</tr>
<tr>
<td>Nov-Dec</td>
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<td>0.0017</td>
<td>0.32</td>
<td>-0.35</td>
<td>0.019</td>
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</tr>
<tr>
<td>May-June</td>
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<td>0.39</td>
<td>0.002</td>
<td>0.041</td>
<td>-0.003</td>
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<td>July-Aug</td>
<td>0.12</td>
<td>0.21</td>
<td>0.014</td>
<td>-0.0045</td>
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<td>0.95</td>
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<td>Jan-Feb</td>
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<td>0.011</td>
<td>-0.026</td>
<td>0.55</td>
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<td>Growing Season</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>First freeze</td>
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<td>-0.0030</td>
<td>-0.033</td>
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<td>Deer Density</td>
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<td>0.0016</td>
<td>-0.49</td>
<td>0.091</td>
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</tbody>
</table>

**P. tenuis Infection Risk**

Overall, 2635 white-tailed deer were examined for *P. tenuis* infection, with prevalence ranging from 0.7-35.1% for DMUs located within the range of moose in North Dakota. Prevalence was 31.5% (17/54) in the DMU where the Pembina Hills survey area is located, 12.4% (23/186) in the Drift Prairie DMU, and 12.5% (6/48) in the Turtle Mountains DMU. Among the significant models, growing season precipitation was the best predictor of *P. tenuis* prevalence in white tailed deer, with wetter DMUs having higher prevalence (Table 15). This was followed by growing season length, which was also positively correlated with *P. tenuis* prevalence. Abundance of white-tailed deer was the next best predictor, followed by May-June temperature. Both of these variables were positively related to *P. tenuis* prevalence as well (Table 15). The map of relative infection risk produced using the AIC weights of these models was predominantly a function of growing season precipitation and indicates that relative risk of infection is greatest in the southeastern part of North Dakota moose range, and declines to the west (Figure 21). This map also illustrates that the Pembina Hills survey area is located in an area of relatively high risk habitat, compared to the Drift Prairie.
survey area where moderately risky habitat occurs in scattered patches, and the Turtle Mountains woodlands are abundant, but infection risk is in these habitats is lower (Table 15, Figure 21). The distribution of _P. tenuis_-related moose mortalities agree with the risk map; 36 of the 39 reported mortalities occurred in areas of the state identified as high-risk for the transmission of _P. tenuis_ (Figure 21).

### Table 15

<table>
<thead>
<tr>
<th>Model</th>
<th>β</th>
<th>R²</th>
<th>P</th>
<th>AICc</th>
<th>AICwt</th>
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<tbody>
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<td>Growing season precipitation</td>
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<td>&lt;0.0001</td>
<td>-29.34</td>
<td>0.99</td>
</tr>
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<td>Growing season length</td>
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<td>0.0018</td>
<td>-14.67</td>
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<td>Deer Abundance</td>
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<td>0.19</td>
<td>0.039</td>
<td>-8.36</td>
<td>2.8E-05</td>
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<tr>
<td>May-June temperature</td>
<td>0.13</td>
<td>0.18</td>
<td>0.045</td>
<td>-8.06</td>
<td>2.4E-05</td>
</tr>
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</table>

### Discussion

It has been suggested that annual moose harvest rates should be no greater than 10-12% to allow moose populations the opportunity for growth (Timmerman and Buss 1998). In areas where annual harvest exceeded 20%, hunting-related declines in populations have been documented (Fryxell et al. 1988, Laurian et al. 2000, Messier and Crete 1985). Assuming harvest locations are a reasonable reflection of moose population distributions in the three North Dakota MMUs, then annual harvest in North Dakota may have approached or exceeded levels that permit sustainable moose populations. Importantly, however, North Dakota lacks populations of wolves and bears that constitute important sources of mortality in most other ecosystems where research on moose populations has been conducted (Ballard et al. 1981, Boertje et al. 1996, Gasaway et al. 1983, Messier and Crete 1985). Therefore, moose in North Dakota may be capable of tolerating higher levels of harvest mortality than populations subjected to natural
predation in addition to harvest, although even populations experiencing low predation rates may decline when harvest exceeds 25% (Fryxell et al. 1988). Whether or not the current harvest rates for moose in North Dakota were sustainable, the concentration of harvest locations in and around aerial survey areas suggests that the proportion of the moose population harvested annually in each MMU may have been greater than managers assumed. This may be particularly true in the Pembina Hills where 91% of harvested moose with known locations were killed within or in close proximity to the aerial survey unit (Figure 17), and where annual harvest was as high as 44% of the previous winter’s count. Yet while overexploitation may have played a role in the moose
population decline in the Pembina Hills, it may not have been the only factor. For example, prior to the 1995 population peak, estimated harvest rates for moose exceeded 25%, yet the Pembina Hills population experienced steady growth during this period (Figure 9). Also, despite the closing of the moose hunting season for moose in the Pembina Hills MMU after the 2004 season, the most recent aerial survey indicate that moose are now essentially absent from the area (North Dakota Game and Fish Department, unpublished data).

While overharvest may not have been the only factor to impact moose populations, climate trends and the relationships between climate and moose population growth rate did not support the hypothesis that the moose populations in North Dakota are declining as a result of warmer temperatures. In fact, surprisingly, climate data from the 1965-2005 time series showed a cooling trend in summer temperatures for all three moose survey areas in North Dakota. This trend was likely due to the influence of a wet climate cycle in the eastern part of the state that began in 1993 (Todhunter and Rundquist 2004). This wet-cycle also accounted for increases in May-June precipitation in all three areas (Table 13). These trends contrast patterns seen in northwestern Minnesota, where summers were hotter and precipitation did not increase from 1961-2001 (Murray et al 2006). However, despite differing climate trends in North Dakota compared to those of northwestern Minnesota, moose populations in the Pembina Hills survey area were correlated with climate variables, but with the exception of the relationship to the date of first freeze, these correlations were the opposite of those observed in the Murray et al. study (2006). Further, although all three North Dakota moose survey areas showed fairly similar climate trends (Table 16), only in the Pembina Hills area was population growth
significantly correlated with climate variables, suggesting the possibility that correlations between moose population trends and climate trends in this area were not directly the result of climate trends. Thus, while moose in northwestern Minnesota may have been adversely affected by a climate warming, North Dakota moose populations are not experiencing increasing mortality as a result of increased thermal stress to animals.

Although climate changes may not have resulted in direct impacts to moose population trends in North Dakota, climate may have influenced moose populations through its impact on *P. tenuis* transmission. Modeling of *P. tenuis* risk demonstrated that climate factors, in particular growing season precipitation, were an important determinant of the transmission rate of this parasite. It is known that *P. tenuis* larvae require moist conditions to survive following deposition in deer feces (Shostak and Samuel 1984), and precipitation also likely influences the abundance and availability of terrestrial gastropod intermediate hosts, because snails and slugs are more active and occur in greater numbers in wetter areas (Bickel 1977, Burch 1962). For these reasons, environments in North Dakota receiving the most precipitation likely experience greater *P. tenuis* transmission. Further, this relationship of *P. tenuis* prevalence to precipitation combined with the observed trend of increasing summer precipitation suggests that transmission conditions for this parasite may have improved since the onset of the wet cycle. Likewise, a lengthening growing season may have further enhanced transmission by extending the frost-free period over which gastropods can remain active. Increased *P. tenuis* prevalence in white-tailed deer in North Dakota since the late 1980s supports this idea (Chapter 4), and suggests the possibility that disease exposure for moose may have similarly increased.
In addition to the potential relationship between climate and moose populations, increasing white-tailed deer abundance showed a negative correlation with moose population growth rate in the Pembina Hills and the Drift Prairie areas. While previous studies have shown that moose and deer may overlap in the use of forage resources, there is little evidence that white-tailed deer and moose exhibit strong exploitative competition (Irwin 1975, Kearney and Gilbert 1976, Ludewig and Bowyer, Telfer 1970). When competition does occur, it is most often during winter, but even then it is often limited because the ability of moose to tolerate cold temperatures and deep snow conditions allow them to use areas not accessible to deer (Kearney and Gilbert 1976, Ludewig and Bowyer 1985, Telfer 1970). As a result, competitive exclusion of moose by white-tailed deer in this study seems unlikely. Instead, the observed relationship between white-tailed deer and moose population growth rate may represent the result of apparent competition mediated by *P. tenuis*. Deer density was significantly correlated with *P. tenuis*, and based on annual harvest, white-tailed deer numbers increased markedly after 1980 in all three survey areas. In other populations where *P. tenuis* was postulated as a limiting factor for moose, similar relationships between high deer density and moose population have been observed (Dumont and Crete 1996, Karns 1967, Telfer 1967, Whitlaw and Lankester 1994), leading Whitlaw and Lankester (1994) to conclude that declines in moose populations may occur when deer densities exceed 5 deer/km². Although estimates of deer density were not available for the entire 1980-2005 period, recent aerial survey data indicate that winter deer densities in the Pembina Hills aerial survey area have exceeded 5 deer/km² at least since winter 2000-2001, while winter deer densities in
the Turtle Mountains and Drift Prairie areas have remained below these levels (Jensen et al. 2004, Jensen et al. 2005, Jensen et al. 2007, Johnson et al. 2001).

Risk mapping indicated that *P. tenuis* infection risk was greatest in the eastern part of the state, and these results are corroborated by the locations of *P. tenuis*-related moose mortalities (Figure 20). The spatial variability of *P. tenuis* risk related to climate and habitat distribution also provides a mechanism by which concomitant increases in deer density may have resulted in differential impacts on moose populations in the three survey areas. In the Pembina Hills, where climate conditions and availability of woodland habitat allowed for greater *P. tenuis* transmission, the effects of parasite-mediated competition may have been stronger. The observed relationship between deer density and moose population growth support this idea, as correlations between deer density and moose population growth rates were evident for both the Pembina Hills and Drift Prairie area, yet only in the Pembina Hills, where *P. tenuis* risk was highest, was population growth negative. In the Turtle Mountains, on the other hand, where *P. tenuis* risk was lowest, there was a weak relationship between deer density and moose population growth.

The combined results of this study suggest that the decline of the northeastern North Dakota moose population was a function of high harvest rates and increased exposure to *P. tenuis* due to a wet climate cycle and increasing deer density. While *P. tenuis* may not typically prevent the co-existence of white-tailed deer and moose (Bogacyck et al. 1993, Dumont and Crete 1996, Whitlaw and Lankester 1994), northeastern North Dakota may have represented an exception to this rule because of this interaction between increasing disease incidence and hunting-related mortality. Further,
although the decline of moose in the Pembina Hills area was coincident with that of the north western Minnesota population, population trends observed in North Dakota do not appear to be related to the factors (F. magna and warming temperature) implicated in the northwestern Minnesota decline (Murray et al 2006).

However the results of this study require careful interpretation, as the retrospective nature of this project limited my ability to definitively tie potential mortality factors to moose population declines. Cause-specific mortality of moose was not investigated and, as a result, mortality/morbidity rates associated with P. tenuis infection are not known. Additionally, moose population dynamics may have also been affected by a number of factors not investigated here, such as nutrition, habitat quality, and other pathogens. Any or all of these may have operated independently or interacted with hunting mortality and P. tenuis to produce the observed decline. For example, although F. magna is relatively uncommon in North Dakota moose, it is endemic to the Pembina Hills areas (Chapter3), and may have interacted with P. tenuis to affect pathogen-related mortality. In addition, winter ticks are known to occur in North Dakota, and are also a potential mortality factor for moose (Lanester and Samuel 1998, North Dakota Game and Fish Department, unpublished data). Despite these caveats, I was able to identify important differences in the relationships between moose populations in the three survey areas in relation to climate, deer density, and P. tenuis risk. Pembina Hills moose experienced high harvest rates and were subject to greater P. tenuis risk than their counterparts in the Turtle Mountains and Drift Prairie, and population growth rate in the Pembina Hills was negatively related to precipitation, growing season length, and deer density, while these factor were positively related to P. tenuis prevalence.
Management Implications

Although the proximate factors contributing to the decline of moose in northeastern North Dakota and northwestern Minnesota may have been different, the results of my study agree with those of Murray et al. (2006); at the southern edge of their range, moose face overlap with growing white-tailed deer population, and as a result are likely to experience increased exposure to pathogens such as *P. tenuis* and *F. magna*. Also, while the population dynamics of moose in North Dakota appear to have been related in part to a wet climate cycle, and not climate warming, my results nonetheless demonstrate that climate may influence moose populations. However, while Murray et al. (2006) suggest that climate warming may result in a northward shift in moose range, whether this scenario occurs in North Dakota, as the wet-cycle ends, and hotter and dryer conditions related to longer-term climate change potentially prevail, remains to be seen. These results also illustrate the spatial variability in population dynamics that may exist across relatively short distances, and it should be recognized that these differences may require area-specific management strategies. In North Dakota, I recommend that managers incorporate information on the variability in disease risk and data on moose population distribution when setting moose harvest levels.
APPENDIX I

Number of locations and value of smoothing parameter \((h)\) used for fixed-kernel estimates of seasonal and total home range sizes for moose.

<table>
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<th>Moose</th>
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<th>Home Range</th>
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