POPULATION DYNAMICS OF MOOSE IN THE WESTERN UPPER PENINSULA OF MICHIGAN, 1999-2001

By

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ABSTRACT

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Moose (*Alces alces americana*) are native to Michigan but were possibly extirpated from the entire state by the end of the 19th century. With the goal of reestablishing a self sustaining population of moose in the Upper Peninsula of Michigan, the Michigan Department of Natural Resources (MDNR) translocated 61 moose (59 of which were released) from Ontario, Canada to western Marquette county in the winters of 1985 (n=31) and1987 (n=30). Based on evaluations of potential habitat and optimistic population growth projections the objective was to have a self-sustaining population of 1000 moose by the year 2000. However, population size estimates from aerial surveys conducted in the winters of 1996 and 1997 were well below 1000. To evaluate the possible reasons for the slower than expected population growth, 84 moose were captured and radio-collared in the winters of 1999-2001. Survival of all age classes has been excellent; annual survival of adults was >85% and first-year calf survival >70%. Seventy-four percent of adult cows were pregnant which is lower than the 84% average for moose in North America. In addition, radio-tagged moose, primarily yearlings, have dispersed out of the study area at an annual rate of about 6%. Preliminary indications are that low reproductive output is the likely cause of the slower than predicted population growth.

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Lastly, but most importantly, I thank my wife, Trish, for her love and support and for encouraging me to follow my dreams.

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INTRODUCTION

The Eastern sub-species or Taiga moose (*Alces alces americana*) is native to Michigan and once ranged throughout the entire state, except for the most southwestern portion of the Lower Peninsula (Baker 1983, de Vos 1964, Peterson 1955, Schroger 1942, Wood 1914). Moose were probably never numerous in the Lower Peninsula because of its geographic location at the extreme southern limit of moose range. This factor in combination with habitat degradation and unregulated hunting resulted in the extirpation of moose in the Lower Peninsula by the mid-1880s. The last credible sighting in the Lower Peninsula may have been John Roger's report of a moose at Black Lake in Presque Isle County in 1883 (Wood and Dice 1923, Baker 1983). In an effort to protect any remaining moose in the Lower Peninsula and those in the Upper Peninsula, the Michigan Legislature passed a law in 1889 giving moose full protection.

The Upper Peninsula of Michigan may have supported a substantial moose population prior to extensive human settlement after the American Civil War (1861-1865). However, by the end of the 19th century, despite legal protection, moose in the Upper Peninsula had declined and may have been briefly extirpated. Dramatic changes in habitat from logging and fires, heavy hunting pressure, wolf (*Canis lupus*) predation and diseases were speculated as factors contributing to the population decline (Verme 1984). The last record in the 19th century of a moose in the Upper Peninsula is possibly Hickie's (1944) report of the poaching of a yearling female in the vicinity of Breevort Lake in Mackinac County in 1899. However, periodic sightings of moose in Chippewa, Luce and Schoolcraft counties (Wood and Dice 1923) provides some anecdotal evidence that a remnant population may have persisted in the eastern Upper Peninsula.

According to Baker (1983) the 1st Biennial Report of the Michigan Department of Conservation (MDC) for 1920-1921 estimated that a population of >1000 moose existed in Chippewa and Luce counties. A closer reading however, reveals that this estimate included the large moose herd on Isle Royale (see below). The 1st Biennial Report actually states that a herd of 25 or more moose had been located near the southern boundary of the Lake Superior Forest Reserve in Luce County and that moose had also been seen in western Chippewa county. A decade later in the 6th Biennial Report (1931-1932) the MDC states that the population in Chippewa and Luce counties had increased, although no numbers are given. In addition, sightings of moose had been reported from Alger, Mackinac and Schoolcraft counties in the eastern Upper Peninsula and Keweenaw County in the western Upper Peninsula. It is not clear if the observations in the eastern Upper Peninsula were of moose from a small remnant population or whether the observations were of animals that periodically immigrated from Ontario. Also, the reported sighting in Keweenaw County is questionable because (1) no moose had been reported in any county in the western Upper Peninsula in Biennial reports prior to 1930 and (2) no evidence or sightings of moose in Keweenaw County were recorded during 1954-1983 (Appendix Table 1, Appendix Table 2).

Although moose in the Upper Peninsula of Michigan were fairing poorly, the population on Isle Royale, Michigan – a 544-km^2 island in Lake Superior, 24 km from the Canadian shore – was proliferating. Dr. Adolph Murie (1934) reported that there were at least 1000 moose (~1.84 moose/km^2) on Isle Royale and that the vegetation was severally over-browsed. To reduce the population on Isle Royale with the added benefit of re-establishing moose in the Upper Peninsula, the MDC live-trapped and transported 71 moose (33 adult males, 38 adult females) to the Upper Peninsula in the winters of 1935, 1936, and 1937. Thirty-four moose were released in the Cusino Game refuge in Schoolcraft County, 17 in the Escanaba River tract (Marquette County), 18 on the Keweenaw Peninsula, and two were given to the Detroit Zoological Park (Hickie 1944). In addition, 6 moose were kept in captivity at the Cusino Game Refuge for life history studies (Verme 1970). The 9th MDC Biennial Report (1937-1938) recorded 108 sightings of moose following these releases. Furthermore, observations or evidence of moose had been recorded in all counties of the Upper Peninsula except Gogebic and Ontonagon counties by 1941. However, by the end of World War II (1942-1946) the population had again declined (Verme 1984).

Moose are not mentioned again until the 21st (1961-1962) Biennial Report, which notes an increase in observations, again primarily in the eastern Upper Peninsula. Additionally, 2 small groups of moose were purported to exist in northern Marquette and northern Iron counties in the western Upper Peninsula. However this is not substantiated by the observations of moose documented by Verme (1984) who reported only 9 observations of moose between 1961-1966 in the western Upper Peninsula (Appendix Table 1). Through the remainder of the 1960's and into the early 1970's Biennial Reports produced by the MDC (renamed the Michigan Department of Natural Resources [MDNR] in 1968) are nearly identical. Paraphrasing these reports, "Observations or evidence of moose continue to be reported from most counties of the Upper Peninsula, primarily in Chippewa, Luce and Mackinac counties in the eastern Upper Peninsula". No attempts were made to actually estimate the moose population size during this period, however, the 23rd Biennial Report (1965-1966) states that "...25-50 animals seems to be a reasonable figure".

Observations of moose appeared to increase in the entire Upper Peninsula after 1966. However it is likely that the increase in tourism following completion of the Mackinac Bridge in 1957 was responsible, rather than an actual increase in moose numbers. Evidence supporting this is that only 14 observations of calves, 10 of which were from the eastern Upper Peninsula, were made during 1961-1983 (Appendix Table 1, Appendix Table 2) suggesting that reproduction was low. From 1967 to 1983 sightings and/or evidence of moose averaged approximately 13 per year in the eastern Upper Peninsula and 3 per year in the western Upper Peninsula (Appendix Table 2).

Despite the failed initial attempt to re-establish moose to the Upper Peninsula the idea was kept alive by MDNR Regional Wildlife Biologist Ralph

Bailey (deceased June 2001) (Verme 1984). However, it was not given serious consideration until the white-tailed deer (*Odocoileus virginianus*) density in the Lake Superior watershed had decreased to acceptable levels. White-tailed deer are the normal definitive host of two parasites, the large American liver fluke (*Fascioloides magna*), and meningeal or brain worm (*Parelaphostrongylus tenuis*), that are potentially harmful to moose. Moose acquire these parasites by inadvertently ingesting the intermediate host (aquatic snails in the case of liver flukes and terrestrial gastropods in the case of brain worm) harboring the infective form of the parasite along with their food. It is speculated that transmission of these parasites to moose is correlated with white-tailed deer densities. In Maine, Gilbert (1974) found a positive correlation between deer density and prevalence of moose infected with brain worm. In addition, moose declines in Minnesota, New Brunswick, Nova Scotia, and Maine occurred when white-tailed deer densities exceeded 5.0/km^2 (Whitlaw and Lankester 1994a, 1994b). Fewer white-tailed deer may reduce the incidence of moose contacting and being infected by these parasites. However, liver flukes alone have not been shown to be detrimental to moose and the relationship between white-tailed density, the prevalence of moose infected with brain worm and the impact of brain worm on moose populations is more subtle than previously hypothesized (Gilbert 1992, Nudds 1990, Nudds 1992, Whitlaw and Lankester 1994a, 1994b).

To assess potential moose habitat in the Upper Peninsula, H. Cummings from the Ontario Ministry of Natural Resources (OMNR), Ontario, Canada was invited to conduct ground and aerial surveys in the winter and fall of 1972. He determined that available habitat in the entire Upper Peninsula could probably support a population of approximately 1000 moose. Additionally, he reported that available habitat in the Tracy Creek drainage (an area west of the city of Marquette and south of State route 28) could likely support 500 moose (MDNR 1974). A decade later (October 1982) M. Wilton of the OMNR conducted a more thorough analysis of potential moose habitat. Based on 10 criteria (e.g., aquatic feeding sites, human activity), the Lake Michigamme area in the western Upper Peninsula was rated the highest. This was primarily due to the greater topographic relief than in other areas analyzed, and the good interspersion of summer and winter habitat (Wilton 1982).

Finally, in January-February 1985, the MDNR translocated 28 adult ($\geq$2.5-years of age) and 3 yearling moose (21 females, 10 males) from Algonquin Provincial Park (APP) in Ontario, Canada to a 1,540 km^2 area north of Lake Michigamme in the western Upper Peninsula (Figure 1). Only 29 moose were actually released, 2 cows that developed complications related to the recycling of carfentanil, the drug used to immobilize moose in Ontario, died 3-days after arriving in Michigan (Schmitt and Aho 1986). One died after aspirating regurgitated rumen content and the other could not stand, and was euthanized. To facilitate monitoring, each moose was fitted with a motion-sensitive radio-collar (Telonics, Mesa, Arizona) at the staging area in Ontario. At the time of release, the white-tailed deer density in the western Upper Peninsula was approximately 2.9 deer/km^2 (Hill and Pohl 1983) and the incidence of parasite transmission was considered to be relatively low. A second translocation of 30

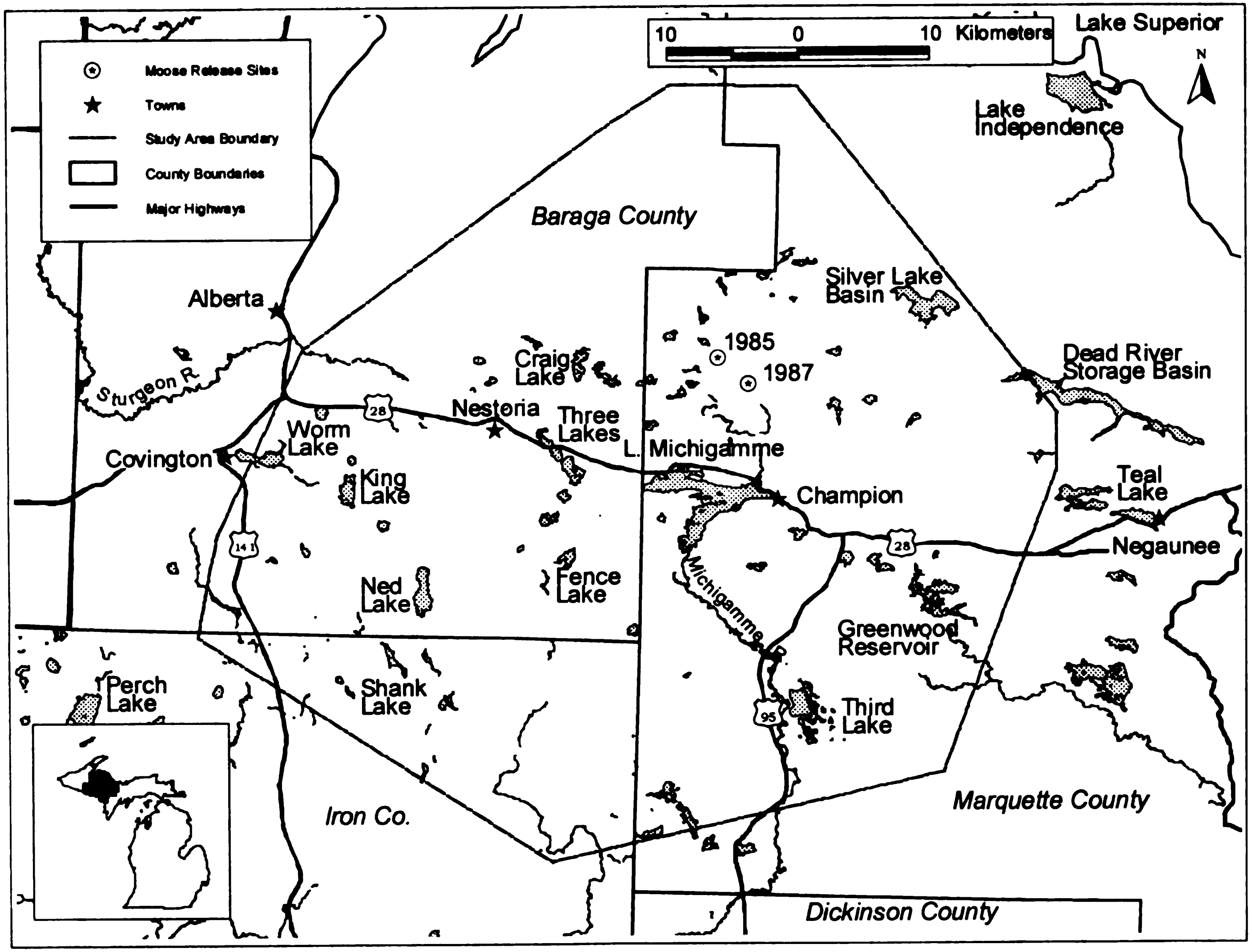

Figure 1. Moose study area during 1999-2001 and 1985 and 1987 moose translocation release sites in the western Upper Peninsula of Michigan.

adult moose (15 cows, 15 bulls) occurred in 1987, prompted by the low pregnancy rate (50%) of radio-tagged females in 1986 (Schmitt and Aho 1986). Two cows died within 1 week after this second release, both were heavily parasitized with hydatid cysts (the larval stage of the tapeworm *Echinococcus grandulosus*) and also suffered from chronic hepatitis, peritonitis, and metritis.

The long-term goal of the 2 translocations was to reestablish a self-sustaining population of moose in the Upper Peninsula of Michigan. Based on Wilton's 1982 report and rudimentary population growth projections (Beyer 2001 personal communication), the objective was to produce a population of 1000 moose by the year 2000 (MDNR 1991a).

For several years following the translocations it was fairly simple to estimate the population. The observed number of calves born in the spring to radio-tagged cows was added to the number of radio-tagged moose that were alive, from which was subtracted the annual number of fatalities of radio-tagged moose. However, as the proportion of radio-tagged moose in the population decreased, a deterministic book-keeping model that incorporated the mortality rates and intrinsic rate of increase from 1985-1990, was used to estimate the size of the population on an annual basis for 1994-1997. Using this method, the 1997 population in the western Upper Peninsula was estimated at 494 moose. (Figure 2). In addition, POP-II (Fossil Creek Software, Fort Collins, CO), a population modeling computer program was used to estimate the population (Figure 2). POP-II projected a population of >850 moose by the year 2000 (Aho et al. 1995).

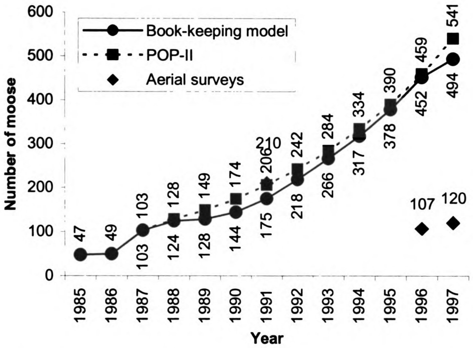

Figure 2. Moose population size estimates for 1985-1997 in the western Upper Peninsula of Michigan based on a deterministic book-keeping model, POP-II, a population modeling computer program, and aerial surveys conducted by the MDNR in 1991,1996, and 1997.

Because it is not feasible to maintain a statistically adequate sample of radio-tagged animals indefinitely, other methods are used to estimate wildlife populations. The most practical method for estimating moose numbers is to count them on their winter range from a fixed-wing aircraft (Timmermann 1993). In January-March 1991, the MDNR conducted an experimental aerial survey of moose in the Upper Peninsula using techniques developed by the Ontario Ministry of Natural Resources (Aho et al. 1995). Although the entire Upper Peninsula was sampled, no moose were seen in the eastern Upper Peninsula. Based on this survey the population was estimated at approximately 210 moose (Figure 2, MDNR 1991b), a value higher than the estimate generated by the book-keeping model (175 moose). To make the aerial surveys more rigorous, and to account for unseen animals, a stratified sampling scheme and sightability model were developed (Drummer and Aho 1998). Use of the new survey methods produced population size estimates of 107 moose in the winter of 1996 and 120 in the winter of 1997. Values much lower than those generated by the book-keeping model (1996, n = 452; 1997, n = 494, Figure 2). At the time there was no evidence of a massive die-off of moose (MDNR 1997), so the differences between the estimation methods could not be readily explained.

The stimulus for the current research grew out of the inability of the MDNR, after extensive evaluation, to explain the discrepancies between the population size estimates from the aerial surveys and those produced by the book-keeping model. In addition, recent declines in moose populations in the Great Lakes region, specifically northwest Minnesota (Cox et al. 1997) and Ontario, Canada, have MDNR biologists concerned that factors effecting these populations are, or will eventually, impact the moose population in Michigan. Only through a better understanding of the population dynamics of moose in the Upper Peninsula can these issues be addressed. To accomplish this, data must be collected on the three factors that control population growth, (1) births, (2) deaths, and (3) emigration/immigration. The use of radio-tagged animals is a widely accepted practice for gathering this information. Movement of animals into the population (immigration) is assumed to be negligible and will not be determined. This study of moose population dynamics will produce quantitative measures of birth, death, and dispersal rates, and will provide the basis for developing a scientifically sound management objective for the moose population in the western Upper Peninsula of Michigan.

RESEARCH OBJECTIVES

The data obtained from this study will help the MDNR Wildlife Division (MDNR-WD) develop a more scientifically rigorous moose population model and provide a better understanding of the spatial movements of moose. This information will help guide future management strategies and set realistic objectives for the moose population in the western Upper Peninsula of Michigan. The main objective of this study is to quantify the population dynamics of moose in the western Upper Peninsula by:

1) Estimating pregnancy rates and natality of cow moose,
2) Estimating sex- and age-specific survival rates of moose,
3) Estimating dispersal rates of moose, and
4) Identifying potential limiting factors of moose population growth.

STUDY AREA

The research was conducted in the western Upper Peninsula of Michigan between January 1999 and June 2001. The core study site (defined as the area within which >95% of all radiotelemtry relocations were obtained) included portions of Baraga, Iron, and Marquette counties and covered an area of approximately 3000 km^2 (Figure 1). This area was chosen because both the 1985 and 1987 release sites are within the area and it has the greatest known density of moose in the Upper Peninsula.

The western Upper Peninsula is bounded to the north by Lake Superior and to the south and west by the state of Wisconsin. Approximately 90% of the western Upper Peninsula is wooded, primarily in secondary growth forests. During the mid- to late 1800's iron mining and logging were the primary enterprises. Today, recreation and timber production are the most important land uses.

The Upper Peninsula is part of the deciduous/coniferous ecotone or "northern-hardwood boreal forest" (Theberge and Theberge 1998), an area of transition between the northern boreal forests and the more temperate deciduous woodlands to the south. This is reflected in the heterogeneous composition of forests throughout the region.

In the western portion of the Upper Peninsula, northern hardwoods forests lacking American beech (*Fagus grandifolia*, except along the Lake Superior shoreline) dominate upland areas. Exposed rocky ridges support scattered white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and trembling aspen (*Populus tremuloides*) which are often disturbed by windthrow and lightning strike caused fires. On moderately to poorly drained sites balsam fir (*Abies balsamea*), black ash (*Fraxinus nigra*), eastern hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), trembling aspen, white spruce (*Picea glauca*), and yellow birch (*Betula alleghaniensis*) may be found either as mixed conifer-hardwoods or pure conifer or hardwoods stands. A variety of wetlands including conifer bogs, hardwood swamps, conifer swamps, and speckled "tag" alder (*Alnus incana*) thickets occur where bedrock is at or near the surface. Large contiguous stands of willow (*Salix spp.*) – often an important moose food item – found along river and stream banks are conspicuously absent, although small scattered patches do occur.

Two distinct physiographic regions (Albert 1995) – the Michigamme Highlands (Subsection IX.2) to the north and northeast and the Upper Wisconsin/Michigan Moraines (Subsection IX.3) to the south and southwest – divide the study area.

Granite bedrock at or near the ground surface dominates much of the Michigamme Highlands Subsection. Outwash plains and steep sandy plains are present where gaps in the bedrock exist. The terrain consists of a mosaic of low (< 15.0 m) rocky knolls in the southern parts of the Subsection and higher (160-250 m) exposed ridges in the Huron Mountains to the north. Numerous lakes and swamps occur in glacially formed depressions in the bedrock. Elevation ranges from 184 to 604 m.

The Upper Wisconsin/Michigan Moraines Subsection consists primarily of course-textured (sand and sandy loam) end moraines. Steep, well-drained ridges; deep, steep-sided kettle lakes, and poorly drained depressions characterize the terrain. Elevation ranges from 183 to 595 m.

Because of the absence of a large body of water to its south, the climate of the western Upper Peninsula is more continental than that in the eastern Upper Peninsula. The lack of lacustrine moderation results in a greater variation in seasonal temperatures. In addition, average interior winter temperatures are often 9-12 °C colder than those along the Lake Superior shoreline. Thunder-storms are also more likely in summer. Average annual rainfall at Champion, Michigan from 1951 to 1980 was 85 cm; sixty-three percent (54 cm) of which fell during the April to September growing season (Berndt 1988). The following temperature and precipitation readings were recorded at Van Riper State Park in Champion, Michigan from 1999 to 2001. In January, the average daily minimum temperature was -20.2 °C, average daily maximum temperature was -4.3 °C. Average daily minimum and maximum temperatures in July were 8.4 and 26.5 °C, respectively. In comparison, the average daily minimum temperature for 1951-1980 at Champion, Michigan in January was -17.5 °C and the average daily maximum temperature was -6.0 °C. Also, for the same period, the average daily minimum temperature in July was 10.0 °C and the average daily maximum temperature was 25.8 °C (Berndt 1988). Average seasonal snowfall for 1999-2001, all of which occurred between November-April, was 211.5 cm. Mean annual snow-fall at Champion, Michigan during 1951-1980 was 350.5 cm. Mean daily snow depth on the ground at Van Riper State Park during January-February was 57 cm in 1999, 24 cm in 2000 and 54 cm in 2001.

A number of animal species have the potential to positively or negatively impact moose. Predators of moose, primarily calves, are black bears (*Ursus americana*) and wolves. At present the black bear population in the Upper Peninsula is estimated at >12,000 and the increasing wolf population is estimated at 200-250. Ponds created from beaver (*Castor canadensis*) dammed rivers and streams allow for escape from summer heat and insects as well as providing aquatic vegetation, an important summer food source. White-tailed deer may have the greatest potential to negatively impact moose because they are the normal definitive host of the meningeal or brain worm; 50 to 90 percent may be infected, but signs of the disease are rare (Lankester and Samuel 1998). In moose, however, it can cause “moose sickness” (Parelaphostrongylosis or Cerbrospinal Nematodiasis) which manifests itself in severe neurological disorders (Anderson 1964) and often results in death.

METHODS

Capturing and radio-tagging

Hawkins & Powers Aviation, Greybull, Wyoming captured moose via net-gunning from a helicopter (Hughes 500 or Bell Long Ranger L-3). Captures were conducted in January-February 1999, January 2000, and February 2001. MDNR Forest Division (MDNR-FD), MDNR-WD, and Michigan State University (MSU) personnel provided air and ground support. For at least a week prior to each year's capture effort the study area was surveyed from fixed-wing aircraft (Cessna 172, 182 or 201) flown by MDNR-FD pilots to find and record locations of moose. Upon arrival of the capture crew these locations were re-flown to look for potential moose targets. When a moose was spotted its coordinates (Latitude/Longitude in decimal degrees) were stored (i.e., a waypoint was recorded) in a Precedus Global Positioning System (GPS) unit (UPS Aviation Technologies, Salem, Oregon). These coordinates were then radioed to the helicopter pilot who attempted to drive the animal to a suitable netting location (e.g., frozen swamp, lake, or pond). For the safety of moose and netting crews steep hills, cliffs, and open rivers and streams were generally avoided.

Exclusively MDNR and Hawkins & Powers Aviation personnel did all handling of captured moose. Moose were fitted with radio-collars (transmitters) equipped with 4-hour motion sensitive switches (Telonics, Inc., Mesa, AZ) and ear tags were attached to both ears. Blood was drawn from the jugular (preferred) or femoral artery of all moose to assess winter health condition and to determine the pregnancy status of cows. Health condition was evaluated through measures of hemoglobin (Hb) and packed cell volume (PCV) in whole blood and calcium (Ca), copper (Cu), iron (Fe), magnesium (Mg), phosphorous (P), potassium (K), sodium (Na), selenium (Se), vitamin A, and zinc (Zn) in blood serum. Pregnancy status was determined through assays of blood serum for pregnancy specific protein B (PSPB) and progesterone concentrations. Fecal samples were collected to measure glucocorticoid concentrations as an indicator of physiological stress (Millspaugh et al. 2001) and to test cows for pregnancy through assays of fecal progesterone concentrations. A 2-cm diameter patch of hair (including shafts and follicles) was plucked from the shoulder hump of each captured animal. Hair samples were archived for future determination of elemental deficiencies and accumulation of toxins (Flynn et al. 1975), and possible genetic profiling. The following data were recorded for each captured moose: (1) coordinates of capture location, (2) estimated age, (3) sex, and (4) physical examination score (Appendix Table 3). Because the capture process can be highly stressful, each animal's body temperature (normal = 38.4-38.8 °C), pulse rate (normal = 70-91 beets/min), and respiration rate (normal = 13-40 breaths/min) were closely monitored. If excessive stress or overheating was detected, moose were quickly radio-tagged, released, and closely observed over the next several days for continuing problems.

Radio-telemetry relocating

Aerial relocations

Following release, all radio-tagged moose were relocated at least weekly throughout the year from a fixed-wing aircraft (Cessna 172, 182 or 201) equipped with radio-telemetry tracking equipment (side-facing, 2-element yagi antennas mounted to each wing strut, connected by coaxial cable to a switchbox in the cockpit). Transmitters were located and point locations of detected moose were recorded as waypoints (map datum: WGS-84, Latitude/Longitude: decimal minutes) in a Precedus GPS. If radio-tagged moose were relocated near open areas (e.g., open water, wetlands or logging clear-cuts) visual confirmations were attempted. In addition, if untagged moose were seen, their location, age and sex (if possible) were recorded. Vegetation cover type and moose activity (bedded, feeding, or moving) were also noted.

Ground relocations

Radio-tagged moose were also approached on the ground to collect fecal samples, and to determine calving status and calf survival (see below). Before going into the field the most recent waypoint recorded for the targeted radio-tagged moose was converted to Universal Transverse Mercator (UTM) grid coordinates and plotted on the appropriate 1:25000 United States Geological Survey (USGS) quadrangle map.

In the field, radio-telemetry equipment was used to take at least three directional bearings, which were then drawn on the USGS quad map to establish a more precise location. To determine the approximate distance to the targeted moose the UTM coordinates of this location were recorded in a Garmin GPS III+ unit (Garmin, International, Inc., Olathe, Kansas).

After moving to within 0.15-0.30 km of the targeted moose, it was approached more closely by directionally homing-in on the transmitter signal.

Transmitter signal strength, change in angle, approximate distance to the targeted moose, and auditory cues (e.g., breaking of saplings, moose vocalizations) were used to determine proximity to the animal. Visual sightings were always attempted to verify the identity of the radio-tagged moose and to make health condition and behavioral observations. When collecting fecal samples, after a sighting was made or evidence (e.g., tracks, beds) of the targeted moose was found, observers walked 100-150 meters in each of the four cardinal directions (N, S, E, W) to determine if other moose or their sign were present in the area. Fecal pellets were collected only if we were certain of the identity of the moose that had deposited them. Fecal pellet size (Cox et al. 1997), track size, stride length, ventral surface drag marks, and bed dimensions were used to differentiate between adults and calves. The following information was recorded at the collection site: GPS coordinates, estimated position error (EPE), vegetation cover type and dominate plant species, snow depth (cm), bed dimensions (cm), and elevation (m).

Survival and mortality

Survival monitoring of radio-tagged moose (i.e., listening for a slow pulse rate [alive=~60 beats/sec.] or a rapid pulse rate [dead=~120 beats/sec.] from each transmitter) was generally conducted once or twice a week from a fixed-wing aircraft. If inclement weather or other priorities (e.g., fire patrols, aircraft maintenance) prevented us from flying, ground monitoring of transmitters was conducted if >1 week had passed since the previous survival check. Survival monitoring of calves seen with radio-tagged cows during spring calf checks was done at monthly intervals as described above (see Ground relocations).

Whenever a mortality pulse signal was heard during an aerial relocation flight the signal was homed-in on, a GPS waypoint was taken, and a visual of the animal was attempted. As soon as possible the transmitter emitting the signal was approached on the ground. While in the field, a transmitter emitting a mortality pulse signal was approached immediately by homing-in on the signal.

Upon verifying that the moose was dead, the surrounding area was examined for signs of predators (Roffe et al. 1994), evidence of humans, evidence of behavior associated with *P. tenuis* (Anderson and Lankester 1974), or other possible causes of death. Photographs of the surrounding area were also taken prior to approaching the carcass. If possible the whole carcass was transported to the MDNR Rose Lake Diagnostics Lab (RLDL) in East Lansing, Michigan. In most instances this was not feasible and a gross field necropsy was performed. When conducting necropsies we followed the guidelines of Nettles (1981). Depending on the degree of decomposition and amount of scavenging the following items were examined and collected: the entire head, 1st incisors, femur, liver, heart, lungs, kidneys, reproductive tract of females, and samples of hide, feces, and blood. In addition, photographs of abnormal-appearing tissues, organs, or other abnormalities (Roffe et al. 1994) were taken. Additional information recorded included date, time of day, GPS location, elevation, vegetation cover type, dominant plant species, weather conditions, snow depth (when applicable), presence or evidence of insects or parasites (e.g., ticks

(*Dermacentor* spp., liver flukes), physical condition score (Appendix Table 3), and preliminary cause of death.

All samples were sent to the RLDL for examination and analysis. First incisors were sectioned and cementum annuli counted to estimate ages of dead moose (Sargeant and Pimlott 1959, Gilbert 1966). The meninges or membranes covering the brain were inspected for presence of meningeal worms, and moose livers were sectioned and inspected for large American liver flukes. Assessment of subcutaneous and visceral (e.g., kidney) fat deposits, physical condition score (Appendix Table 3) and chemical assays of femur bone marrow were used to evaluate the nutritional condition of moose near time of death (Neiland 1970, Mech and DelGiudice 1985). Causes of death were classified as accidents, unknown, disease or predation.

Survival rates of moose with 95% confidence intervals (95% CI) were calculated using MICROMORT, a DOS-based microcomputer program developed by Heisey and Fuller (1985) which incorporates the Mayfield survival estimator (Mayfield 1961, 1975). MICROMORT uses the Taylor series method (which is based on symmetric intervals about the log-transformed survival function) to calculate 95% CI's, therefore, the 95% CI's were truncated to lie between 0 and 1. The Mayfield estimator calculates the interval survival rate ($\hat{S}_i$) for the period of interest (L) as:

$$\hat{S}_i = 1 - \frac{\text{number of deaths in the period}}{\text{total exposure intervals}}$$

where the total exposure intervals (e.g., months) is equal to the sum of all intervals each animal is at risk of death (i.e., the number of intervals from which an individual enters the study, t_0, until it is last observed t_i). The period survival rate ($\hat{S}_p$) is then $\hat{S}_p = \hat{S}_i^L$. When used with radiotelemetry data the Mayfield model assumes that the survival rate remains constant over the period of interest (Trent and Rongstad 1974). To reduce the bias associated with relocation probability (Bunck et al. 1995), we attempted to check (listen for dead or alive signal) each individual frequency at least weekly (see above). However, if flights were shortened because of scheduling constraints or inclement weather we tried to check at least 90% of the radio-tagged animals (Kenward 2001) during the flight with the remainder being checked as soon as possible. In addition to constant period survival, all survival models require these additional assumptions: (1) radio-collars do not impact an animals' fate, (2) the exact time of death of each animal is known, (3) individual animals are independent, (4) the survival function of newly radio-tagged animals is equal to that of previously radio-tagged animals, (5) radio-tagged animals are randomly sampled, and (6) censoring of radio-tagged animals is random (Winterstein et al. 2001). Finally, because the Mayfield estimator uses the total period (e.g., animal months) an individual is at risk of dying, it permits staggered entry (i.e., different start times or t_0) (see Pollock et al. 1989) of newly radio-tagged animals.

Annual, summer and winter survival rates of radio-tagged adult (≥ 2-years of age) and yearling (13-24 months of age) moose were calculated. Because adult and yearling moose were checked weekly I initially calculated a weekly-interval survival rate. This weekly rate was then used to calculate a monthly (the period of interest) rate, over which survival was assumed to be constant. Annual (12 month) and seasonal (6 month) survival rates were then equal to the product of the rate for each month (e.g., $\hat{S}_{Annual} = \hat{S}_{June} * \hat{S}_{July} * \ldots * \hat{S}_{May}$). Annual and seasonal adult moose survival rates were also determined for bulls and cows separately. Annual survival rates were calculated for the biological year from 1 June-31 May. Winter was defined as 1 November-30 April and summer as 1 May-31 October. The season starting and ending dates roughly correspond to the first freezing temperature in the fall and the last freezing temperature in the spring.

Survival rates were calculated jointly for radio-tagged and un-tagged calves (<12 months of age) of radio-tagged cows seen each spring. So as not to positively bias calf survival rates, calves radio-tagged in the winter but not previously seen in the spring of that year were not included in survival calculations. Calf survival was calculated for the first-year of life and for two periods, 1 June-30 November (birth to 6 months of age) and 1 December-31 May (6-12 months of age). These periods correspond with times when calves are most vulnerable to black bear and wolf predation in the first period and wolf predation in the second (Van Ballenberghe and Ballard 1998). Although, survival of radio-tagged calves was checked at weekly intervals, survival of un-tagged calves was checked only monthly. It was therefore necessary to assume that calf survival was constant within the 0-6 month and 6-12 month periods. First-year calf survival was then equal to the product of the rate from both periods.

Moose radio-tagged after the start of the biological year (1 June) or seasonal period (winter = 1 November, summer = 1 May) entered the study on the day they were radio-tagged. Except for moose that were radio-tagged in January-February 1999 which entered the study on 1 June 1999. The date of death of radio-tagged moose was estimated at halfway between the last recorded live signal and the date that the moose was first known to be dead (Mayfield 1961, 1975). Determining dates of death for un-tagged calves was not as straight forward. If the radio-tagged cow of an un-tagged calf died during the calf's first 6 months of life, it was assumed that the calf did not survive and it was assigned the same date of death as the cow. If a radio-tagged cow previously attended by an un-tagged calf was found alone for two consecutive months the calf was considered to have died unless it had attained an age of at least nine months. In this case the un-tagged calf's date of death was estimated at halfway between the last date it was seen with its cow and the date that the cow was first seen alone. Un-tagged calves not seen with their radio-tagged dams after attaining the age of 9 months (the earliest time of cow-calf separation) were assumed to have survived the entire year.

Survival rates of adults were compared between years, seasons, and sexes. Yearling survival rates were compared between years and seasons and also to adult survival rates. First-year and interval (birth to 6 months of age, 6–12 months of age) survival rates of calves were compared within and between years. In instances where sample sizes were adequate (>30), comparisons between survival estimates where made with a simple approximately normal test statistic based on the equation:

$$Z = \frac{\hat{S}_1(t_1) - \hat{S}_2(t_1)}{\sqrt{\mathrm{Var}\ \hat{S}_1(t_1) + \mathrm{Var}\ \hat{S}_2(t_1)}},$$

where $\hat{S}(t_1)$ is the estimate of the first survival curve at time t_1 and $\hat{S}_2(t_1)$ is the estimate of the second survival curve at time t_1 (Pollock et al.1989). Statistical significance was accepted at $P \leq 0.05$.

Movements

<u>Home range size and dispersion</u>

Relocations (radio-fixes) obtained during weekly flights, winter fecal sample collection, spring natality determinations and calf survival monitoring were used to (1) estimate annual and seasonal home range size, (2) monitor home range development and (3) differentiate exploratory movements from permanent dispersal. To standardize radio-fixes collected in different coordinate systems (e.g., UTM, Latitude/Longitude) all were converted to the Michigan GEOREF coordinate system.

Annual (1 May-30 April) and seasonal (summer: ~1 May-31 October, winter: ~1 November-30 April) home range sizes were estimated using the minimum convex polygon (MCP; Mohr 1947) and fixed kernel (FK; Worton 1989) approaches. The Animal Movement Analyst Extension (AMAE; Hooge et al. 1999) to ArcView® (Environmental Systems Research, Inc., Redlands, California) GIS was used to analyze these data. The FK smoothing factor was calculated via least squares cross validation (LSCV). I used the FK-95%

utilization distribution (UD) to estimate home range sizes and the FK-25% UD to estimate the center of seasonal home ranges, from which distances between seasonal ranges could be determined. If the FK-25% UD resulted in more than one home range polygon, the distance between the centers of the multiple home ranges were averaged. Annual and seasonal home ranges were estimated only when >19 and >9 relocations per moose respectively, were available. When determining seasonal home ranges, relocations that deviated from grouped relocations were considered transitory points and were excluded from seasonal home range estimates. Moose were considered to be migratory if there was <25% overlap of their seasonal home ranges and ≥2 km between the centers of their seasonal home ranges. The Mann-Whitney *U* test was used to make comparisons among FK-95% UD home ranges. The 100%-MCP method was used to permit comparisons to other studies.

To determine if movements of radio-tagged moose were more or less spatially dispersed at certain times of the year, I calculated the average Euclidian (or linear) distance (AD) between all pairs of relocations for individual adult and yearling moose. AD was calculated annually (May-April) and for 3 periods: summer (May-August), fall (September-December) and winter (January-April). Conner and Leopold (2001) demonstrated that AD was more precise and less biased than the kernel home range method, especially with sparse data. AD was calculated only when >19 relocations annually and >9 per season, per moose were available. Comparisons between annual ADs were made with the Mann-Whitney *U* test. Differences among seasonal ADs were determined using the

Kruskal-Wallis test. Unless otherwise noted, $P \leq 0.05$ was required for statistical significance in all home range comparisons.

<u>Dispersal and home range development</u>

A moose was considered to have dispersed if it moved beyond the boundary of the core study area and remained there until it established a new home range, died, dropped its radio-collar or the study ended. Annual (1 June-31 May) dispersal rates (with 95% CI's) of radio-tagged moose were estimated with the Mayfield estimator (Mayfield 1961, 1975). The Mayfield is a time-to-event model generally used to estimate a survival probability, where death is the event of interest. However, the rate of any event such as dispersal, that can be situated in time can be calculated with the Mayfield estimator. Because moose that dispersed were relocated at approximately monthly intervals it was assumed that dispersal was constant among months. The monthly dispersal rate ($\hat{D}_m$) for the period of interest (L) is then estimated as:

$$\hat{D}_m = \frac{\text{number of dispersers in the period}}{\text{total exposure months}}$$

and the period dispersal rate ($\hat{D}_p$) is then $\hat{D}_p = \left[1-(1-D_m)^L\right]$. All other assumptions of the Mayfield estimator were adhered to when estimating dispersal rates. Dispersal distance was approximated by measuring between the centers of the FK-25% UD of pre- and post-dispersal home ranges. In cases where dispersing moose did not establish a new home range, dispersal distance was measured between relocations obtained prior to, and after detection of dispersal.

Home range development of young-of-the-year was quantified by determining the linear distance (km) between and the percentage of overlap of their cow's home range(s) and the areas they occupied after separation from their cow. Moose were classified as yearlings when they became independent of their cow or they attained their first birthday (7 June, the median birthing date).

Reproduction

Pregnancy determinations

The pregnancy status of recently radio-tagged cows was determined through assays of blood serum for pregnancy-specific protein B (PSPB; Haigh et al. 1993, Stephenson et al. 1995) and progesterone levels (Haigh et al. 1982, Stewart et al. 1985) and assays of fecal material for fecal progesterone levels (Monfort et al. 1993, Schwartz et al. 1995).

PSPB is secreted by the placenta (Reimers et al. 1985) and has been shown to reliably detect pregnancy 40 days after conception in moose. It may also be possible to detect the number of fetuses present using assays of PSPB (Huang et al. 2000). Stephenson et al. (1995) was 100% accurate at diagnosing pregnancy in ten captive moose at the Kenai Moose Research Center (Kenai Peninsula, Alaska) in March using assays of PSPB. In addition, Huang et al. (2000) was 84% correct in categorizing single fetuses and 97% correct in categorizing twin fetuses, using PSPB. Again, at the Kenai Moose Research Center (Kenai Peninsula, Alaska) captive cows carrying twin fetuses had serum PSPB concentrations >365 ng/mL, whereas those with singletons had concentrations <365 ng/mL. Because of its accuracy serum PSPB was used as the primary indicator of pregnancy when available.

Assays of the hormone progesterone are less reliable than PSPB at detecting pregnancy because it is not pregnancy-specific (Huang et al. 2000) Progesterone is elevated during gestation but is also present at lower levels in blood serum of males and non-pregnant females. Blood serum progesterone concentrations of pregnant moose are generally >3.0 ng/mL, while levels for non-pregnant moose are <0.5 ng/mL (Schwartz 1997).

Assays of fecal progesterone are less reliable at detecting pregnancy than assays of PSPB or serum progesterone. However, the method is noninvasive and it is relatively easy to collect fecal samples in the winter. Assays of fecal progesterone can be used to reliably detect pregnancy by the eighth week of gestation (Schwartz et al. 1995). Monfort et al. (1993) was 85% accurate in diagnosing pregnancy in captive moose using fecal progesterone levels. Schwartz (1997) and Monfort et al. (1993) reported that pregnant moose generally have fecal progesterone concentrations >2.0 μg/g, whereas levels in non-pregnant moose are <0.5 μg/g.

Assays of fecal material alone were used to determine the pregnancy status of previously radio-tagged cows. Fecal samples were collected at monthly intervals following the first significant snowfall and continued until snowmelt each season. To reduce the chance of a false-positive or false-negative result we attempted to collect at least two fecal samples from each cow. Fifteen to twenty fecal pellets were collected into a zip-lock plastic bag and kept frozen until analysis. Moose stalking procedures and sampling protocols are outlined above (see Ground Locations).

PSPB assay results, when available, and a cow's calving status were used to determine if a radio-tagged cow was actually pregnant or not. In addition, if a radio-tagged cow was not seen with a calf during spring calf checks or its calving status was unknown it was considered to be pregnant if (1) it had a positive PSPB result and serum or fecal progesterone levels indicative of pregnancy, or (2) it had fecal progesterone levels indicating pregnancy from at least two independent fecal samples. When fecal material was used for pregnancy determinations, measures of fecal progesterone concentrations of non-pregnant cows were used to calculate the 95% upper tolerance limit (95% UTL) of pregnancy (i.e., $\overline{x} + t$-value x SD; Messier et al. 1990). The 95% UTL for serum progesterone was also calculated from serum progesterone levels of non-pregnant cows. The Mann-Whitney *U*-test was used to compare progesterone concentrations between pregnant and non-pregnant cows.

The Conservation and Research Center (CRC, Front Royal, Virginia) of the Smithsonian Institute performed the analyses of fecal samples and blood serum for progesterone levels. BioTracking (Moscow, Idaho) conducted assaying of blood sera for PSPB levels.

Productivity

<u>Natality and Recruitment</u>

To determine annual reproduction and roughly estimate calf birthing dates, radio-tagged cows were observed at least once each year between 15 May-30

June, the approximate moose calving period in Michigan (Verme 1970). Although attempts were made to see all radio-tagged cows, priority was given to those that had positive pregnancy test results (see above). Each radio-tagged cow was approached on the ground until a visual observation of the cow and calf or calves was made or strong evidence (e.g., tracks, beds, fecal material) of a calf or calves was found. Observations of radio-tagged cows and their offspring were also attempted during radiotelemetry aerial re-location flights, but due to heavy vegetative cover were very difficult to make. Pregnant cows that were observed alone at the beginning of the calving period were approached multiple times until their calving status was determined.

Determining the annual recruitment of calves into the adult population was accomplished in the same manner as for calving. We attempted to visually re-locate radio-tagged cows and their offspring from the ground and/or air at monthly intervals beginning 1 July and continuing until calves became independent of their cows, the next seasons calving period began, the radio-tagged cow died, or it was believed that the calf had died. Natality, measured as the number of calves per adult female (calf:cow) was determined each spring after calving (post-calving) and prior to calving the following year (pre-calving) as an index of calf recruitment. The frequency of twinning, which has been shown to be an important indicator of habitat quality and female health condition (Franzmann and Schwartz 1985) was calculated each spring as the number of twins produced divided by the number of radio-tagged cows giving birth.

Population size estimation and projection

Difficulties replicating the book-keeping model developed by the MDNR precluded using it to make comparisons between the population size estimates obtained using survival and reproductive values determined for 1985-1996 and those determined during the current study. Instead, POP-II (Windows™ Version 1, Fossil Creek Software, Fort Collins, Colorado), a population modeling computer program was used to make these comparisons. POP-II is a deterministic, density-independent model that uses age-specific mortality rates (i.e., 1 - survival rates) and age-specific reproductive rates (i.e., the number of offspring per reproducing females or calf:cow ratio) to simulate the dynamics of geographically closed animal populations.

Previous estimates of annual survival of adult radio-tagged moose and survival of calves of radio-tagged cows were derived by the Apparent Percent Success (APS) or Simplistic estimator. Using this approach the survival rate ($\hat{S}$) for a selected period of time is estimated as

$$\hat{S} = 1 - \frac{\text{number of deaths in the period}}{\text{number at risk in the period}},$$

where the number at risk is the initial number of animals at the start of the period (Winterstein et al. 2001). Calf production (and thus the calf:cow ratio) was estimated by relocating radio-tagged cows on the ground and observing calves or finding evidence of calves during May-July each year. Calf survival was determined by relocating radio-tagged cows from the air and looking for their calves during December-January 1985-1995 and April 1985-1988 (Aho et al. 1995). Because reproductive determinations and calf monitoring were temporarily suspended during 1991-1993 and the sample of radio-tagged cows in 1994, 1997 and 1998 was small (<10), estimates of the calf:cow ratio and calf survival rates for 1985-1990, 1995-1996 were used in POP-II. Also, estimates of adult survival were only available for 1985-1989.

Additionally, yearling dispersal ($\hat{D}$) was incorporated in the POP-II population size estimates by increasing the average yearling mortality rate. Comparisons were made between population size estimates using the mean survival and reproductive values collected from 1985-1990, 1995-1996 (MDNR [1985-1996]) to average estimates of survivorship and fecundity obtained during the current study (MSU [1999-2001]). Additional comparisons looked at how changes in calf survival and yearling dispersal affected moose population size estimates. Estimates of the population size were made with the following assumptions (1) a 1:1 sex ratio at birth, (2) only cows $\geq$ 2-years of age reproduce, (3) all cows of reproductive age reproduce (this is necessary because POP-II uses a per cow productivity value), (3) only yearling moose disperse and (4) dispersal is not biased toward either sex.

RESULTS

Capturing and radio-tagging

Seventy-four moose were captured and fitted with 4-hour motion sensitive VHF radio-collars in January-February 1999 (n=26), January 2000 (n=26), and February 2001 (n=22). In addition, GPS collars were placed on four moose (2 bulls, 2 cows) in 2000 and six moose (3 bulls, 3 cows) in 2001. Twelve moose (6 bulls, 6 cows) radio-tagged in 1995 were also part of the initial sample population (Table 1). No moose died or were injured during capture, and no signs of capture myopathy (e.g., muscle stiffness, lethargy) were seen following capture in any year.

Table 1. Sex and age breakdown of moose radio-tagged in 1995, January-February 1999, January 2000, and February 2001 in the western Upper Peninsula of Michigan.

Year	Adults		Yearlings		Calves		
	Bulls	Cows	Males	Females	Males	Females	Total
1995	6	6	0	0	0	0	12
1999	1	12	0	1	8	4	26
2000[a]	3	14	0	1	7	5	30
2001[b]	2	11	1	2	8	4	28
Totals	12	44	1	4	23	13	96

[a]Includes 2 bulls and 2 cows outfitted with GPS radio-collars.
[b]Includes 3 bulls and 3 cows outfitted with GPS radio-collars.

Capture locations of all moose radio-tagged in 1995, and between 1999-2001 appear in Figure 3. All radio-tagged moose that were alive as of 30 June 2001 (the end of this study) are currently being monitored.

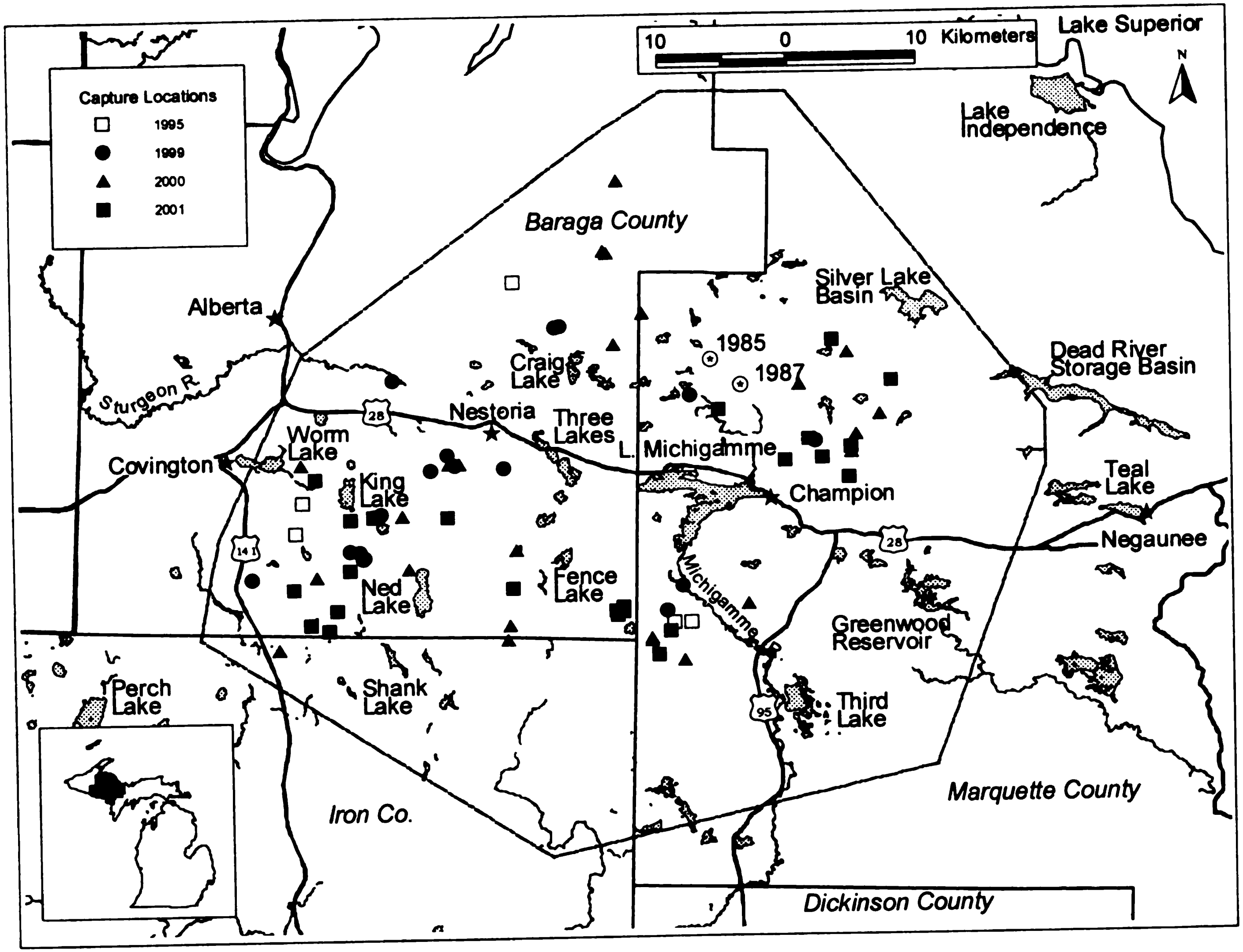

Figure 3. Capture locations of moose radio-tagged in 1995 and during 1999-2001 in the western Upper Peninsula of Michigan.

Radio telemetry relocations

<u>Aerial relocations</u>

Twelve moose radio-tagged in 1995 and twenty-five moose radio-tagged in 1999 were relocated on 1,573 occasions ($\overline{x}$=43 relocations per moose, range=12-59) from February 1999 through May 2001. The mean number of relocations for males (n=14) was 41 and for females (n=23) was 44 during this period. Twenty-nine moose radio-tagged in 2000 were relocated on 668 occasions ($\overline{x}$=23 relocations per moose, range=5-37) from January 2000- May 2001. During this span, the mean number of relocations per males (n=9) was 22, whereas for females (n=20) it was 23. Twenty-eight moose radio-tagged in 2001 were relocated on 143 occasions ($\overline{x}$=5 relocations per moose, range=2-7) from February 2001 through May 2001. The mean number of relocations for males (n=11) and females (n=17) was approximately 5 for the period.

All aerial relocations were obtained during daylight between the hours of 0900 and 1800 (Figure 4). From February 1999 through May 2001, 768 visual observations of moose (586 radio-tagged, 182 un-tagged) were made during 99 of 195 relocation flights. Eighty percent (615 of 768) of all the observations occurred during 57 relocation flights ($\overline{x}$=11 observations per flight, range=1-41) conducted during the winter. The mean number of observations per flight during 42 summer flights was approximately 4 and ranged from 1 to 13. During a 19-day period in late January-early February 2001, when snow and weather conditions were apparently excellent, we observed 234 moose (149 radio-tagged, 85 un-tagged) during 10 relocation flights. Aerial observations of moose

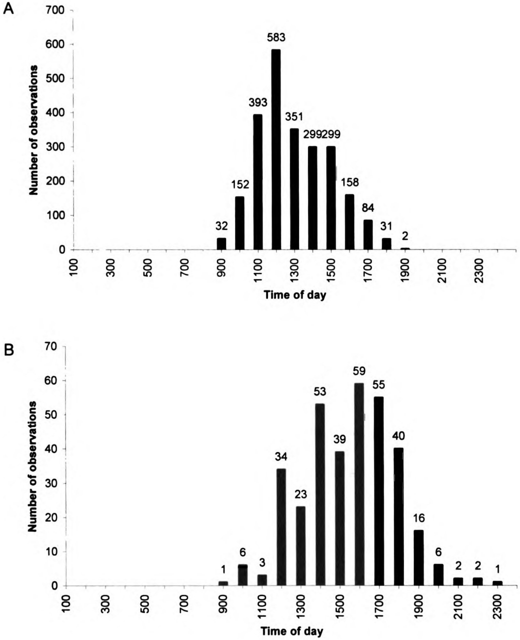

Figure 4. Distribution of radio-tagged moose aerial relocations (A) and ground relocations (B) by time of day in the western Upper Peninsula of Michigan during 1999-2001.

began to increase in the late autumn when leaves were gone and snow cover was present (Figure 5). They peaked during the winter, and the number of observations was greatly influenced by weather conditions. A recent snowfall event and 100% cloud cover at an altitude of approximately 1,000 m. appears to be ideal. The number of moose observed decreased rapidly after snow-melt and sightings continued to decrease as leaves appeared and were at their lowest throughout the summer.

Ground relocations

During the study we approached radio-tagged moose on 340 occasions. We observed 293 individual moose during 190 (59%) of these approaches. Each season as we gained more experience our success rate increased. It was 40% in 1999, 55% in 2000, and 74% in 2001. Ninety-two percent of the animals we approached were females, our primary targets. Males were only sporadically approached and only male calves of radio-tagged cows were approached with any consistency. Moose were approached between the hours of 0900 and 2300, although 87% of approaches occurred after midday (Figure 4).

Survival and mortality

Annual, summer, and winter survival rates for each year for adult and yearling moose are given in Table 2. First-year and interval survival rates for each year for calves appear in Table 3.

Adult and yearling

Between 1 June 1999-31 May 2001, 10 adult (2 bulls, 8 cows) and 5 yearling (3 male, 2 female) radio-tagged moose died. At least one radio-tagged

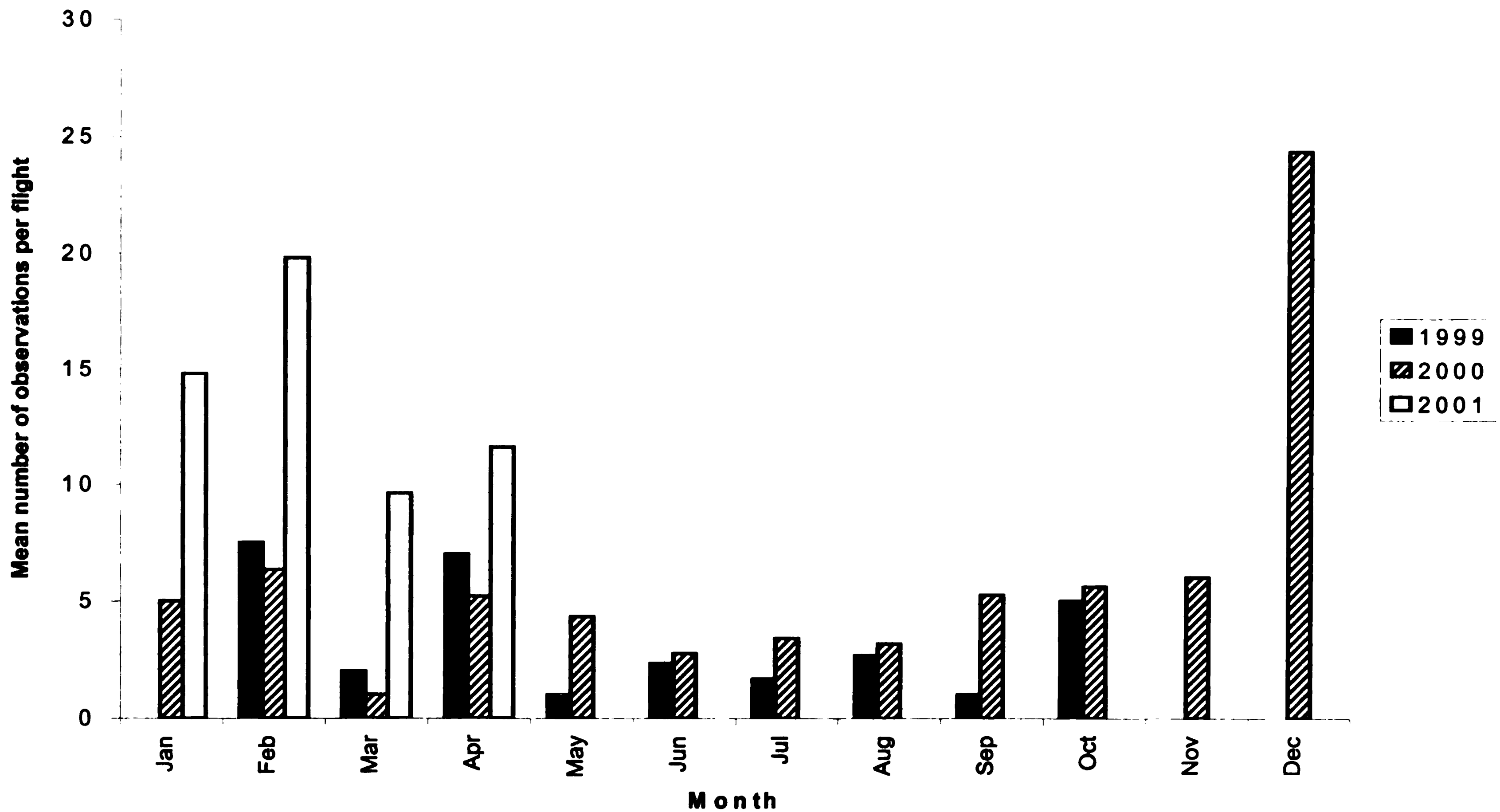

Figure 5. Mean number of moose observations by month during aerial relocation flights when moose were seen in the western Upper Peninsula of Michigan during February 1999-June 2001.

Table 2. Annual and seasonal survival rates of radio-tagged adult and yearling moose studied during 1999-2001 in the western Upper Peninsula of Michigan.

	1999-2000							2000-2001						
Class	$\hat{S}$[a]	SE	No. moose	No. wks.	No. deaths	95% LCI	95% UCI	$\hat{S}$	SE	No. moose	No. wks.	No. deaths	95% LCI	95% UCI
Annual														
Adults	0.880	0.001	42	1570	4	0.776	0.999	0.873	0.001	56	2205	6	0.784	0.974
Yearlings	0.840	0.004	12	547	2	0.660	1.000*	0.800	0.004	16	608	4	0.623	1.000*
Bulls	1.000	0.000	9	92	0	1.000	1.000*	0.857	0.004	15	633	2	0.691	1.000*
Cows	0.840	0.002	33	1170	4	0.707	0.999	0.882	0.001	41	1572	4	0.780	0.999
Summer														
Adults	0.966	0.001	26	683	1	0.902	1.000*	0.933	0.001	43	5017	3	0.863	1.000*
Yearlings	0.914	0.005	11	283	1	0.766	1.000*	0.924	0.004	16	289	1	0.791	1.000*
Bulls	1.000	0.000	7	191	0	1.000	1.000*	0.931	0.005	13	326	1	0.808	1.000*
Cows	0.953	0.002	19	539	1	0.868	1.000*	0.937	0.002	30	776	2	0.857	1.000*
Winter														
Adults	0.934	0.002	43	841	2	0.850	1.000*	0.913	0.001	53	1102	4	0.835	0.999
Yearlings	0.919	0.005	11	268	1	0.779	1.000*	0.867	0.005	14	311	2	0.711	1.000*
Bulls	1.000	0.000	9	210	0	1.000	1.000*	0.921	0.006	14	307	1	0.783	1.000*
Cows	0.911	0.004	32	631	2	0.799	1.000*	0.911	0.002	39	796	3	0.819	1.000*

[a] Survival rates calculated using the Mayfield survival estimator (Mayfield 1961,1975).

* Upper interval truncated at 1.00

Table 3. First-year, 0-6 months of age, and 6-12 months of age joint survival rates of radio-tagged and un-tagged calf moose of radio-tagged cows seen each spring during 1999-2001 in the western Upper Peninsula of Michigan.

	1999-2000							2000-2001						
Classification	$\hat{S}$[a]	SE	No. calves	No. mos.	No. deaths	95% LCI	95% UCI	$\hat{S}$	SE	No. calves	No. mos.	No. deaths	95% LCI	95% UCI
First-year	0.634	0.010	17	157	6	0.439	0.915	0.787	0.007	20	203	4	0.622	0.995
0 – 6 mos.	0.754	0.011	17	87	4	0.568	0.988	0.943	0.006	20	102	1	0.838	1.000*
6 – 12 mos.	0.840	0.012	13	70	2	0.657	1.000*	0.835	0.009	19	101	3	0.678	1.000*

[a] Survival rates calculated using the Mayfield survival estimator (Mayfield 1961,1975).

* Upper interval truncated at 1.00.

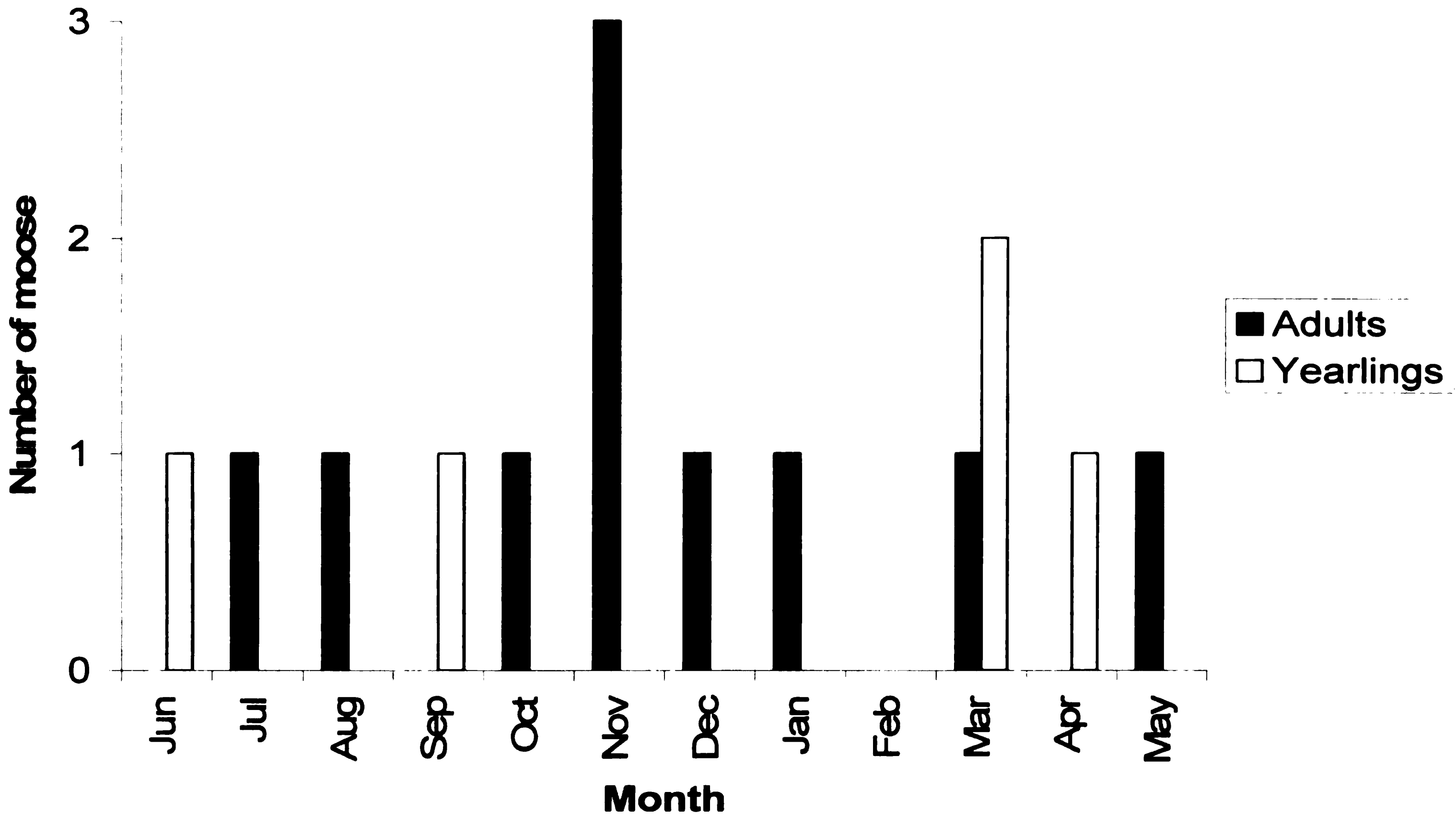

Figure 6. Number of radio-tagged adult and yearling moose deaths by month in the western Upper Peninsula of Michigan during 1 June 1999-31 May 2001.

adult or yearling moose died in every month except February (Figure 6). Estimated ages of dead radio-tagged moose ranged from 1.0 to 13.0 for females ($\bar{x}$=4.75 ±1.24, n=10) and 1.5 to 7.5 for males ($\bar{x}$=3.0 ±1.12, n=5). Forty-eight adult (12 bulls, 36 cows) and twelve yearling radio-tagged moose were alive at the end of the study (Appendix Table 4). The fates of three radio-tagged moose (1 bull, 1 cow and 1 yearling female) that managed to slip their radio collars were unknown. In addition, the fate of three adult moose (1 bull, 2 cows) outfitted with GPS radio-collars were also unknown because the collars were removed to collect the data each contained. Of the remaining 7 moose radio-tagged with GPS collars, 1 bull had his radio-collar replaced with a VHF transmitter and 6 were still wearing their radio-collars when this study ended. The final ground location of each adult or yearling moose that died is shown in Figure 7.

Annual adult survival was 0.88 in 1999 and 0.87 in 2000. Annual and winter survival rates for adults between years (annual: Z=0.089, P=0.4645; winter: Z=0.345, P=0.3677) were not significantly different. Although more adult moose died in the winter (1 Nov-30 Apr, n=7) than in the summer (1 May-31 Oct, n=4) (Figure 6) no difference was detected between winter and summer adult survival rates in either year (1999: Z=-0.554, P=0.3010; 2000: Z=-0.357, P=0.3639). Annual survival of yearling moose (1999 = 0.84, 2000 = 0.80) was less than the annual survival of adult moose in both 1999 and 2000. Winter survival of yearlings in 1999 (0.92) was 6% higher than in winter 2000 (0.87) and in both years, summer survival rates of yearling moose were >0.91.

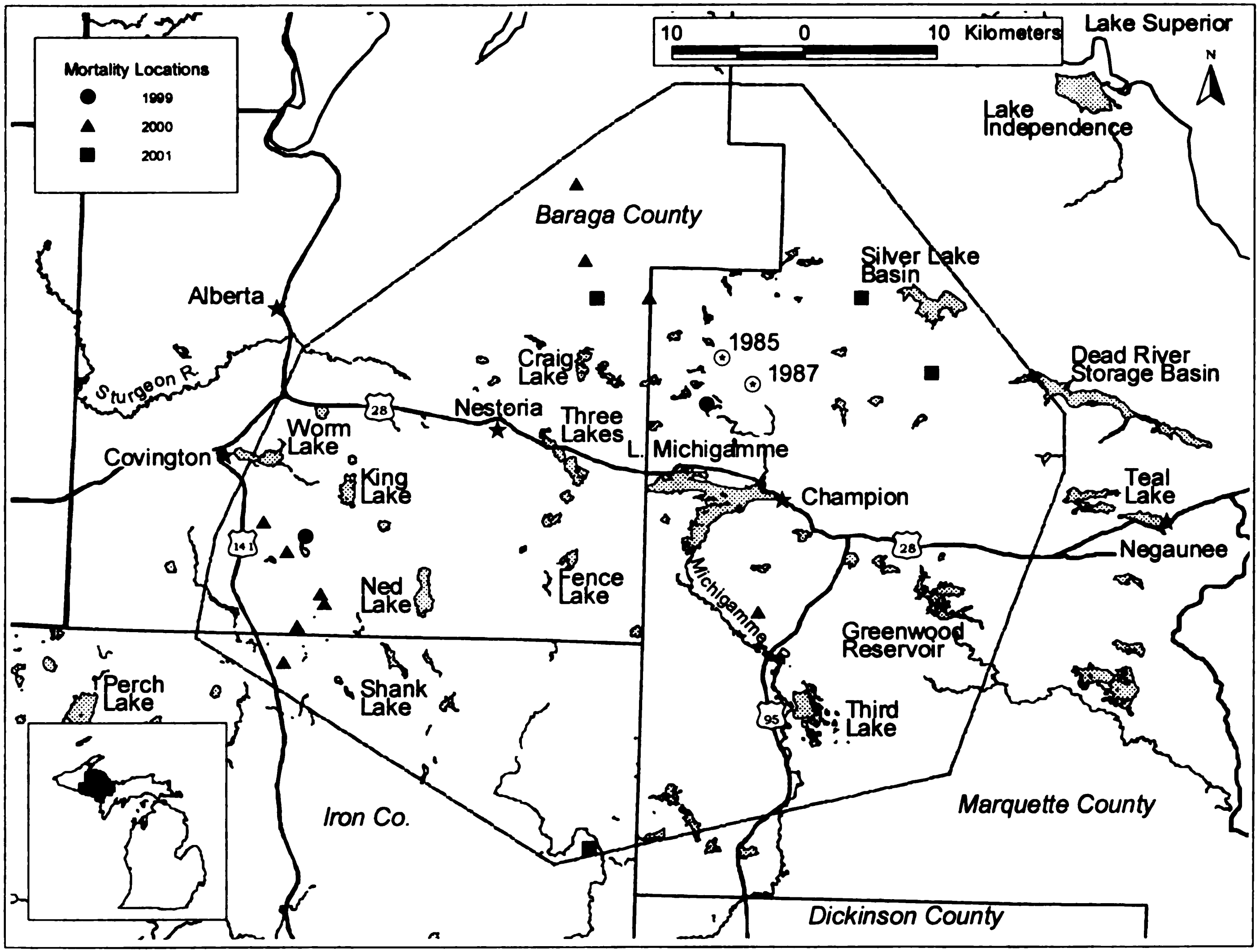

Figure 7. Locations of recovered mortalities of radio-tagged moose within the core study area during 1999-2001 in the western Upper Peninsula of Michigan.

Bull and cow

In 1999, annual bull survival (1.00) was approximately 19% higher than annual cow survival (0.84). In 2000, annual cow survival increased to 0.88 and annual bull survival decreased to approximately 0.86. The high bull survival in 1999 is likely related to the small sample of radio-tagged bulls (n=9) that year. Winter and summer bull survival rates in 2000 were nearly identical (winter=0.93, summer=0.92). Annual survival rates between years (Z=-0.449, P=0.3345) and survival rates between winter and summer in 2000 (Z=-0.398, P=0.3508) for cows were not significantly different. Cow survival in winter 1999 (0.9107) was nearly identical to that in winter 2000 (0.9112). Summer survival rates of cows between years were also very similar (1999=0.95, 2000=0.94).

First-year calf

Seventy percent of calf deaths (1999 n=6, 2000 n=4) occurred in the winter (Nov-April) (Figure 8). However, this seasonally skewed calf mortality pattern could be a result of (1) the frequency (monthly) at which calf survival was checked and (2) the difficulty of detecting calf mortalities shortly after birth. It is interesting to note that all radio-tagged (compared to un-tagged) calves that were seen with radio-tagged cows in the spring survived at least their first year. First-year calf survival in 1999 (0.63) was 20% lower than in 2000 (0.79).

Calves 0-6 months of age

Sixty-seven percent (4 of 6) of calf mortalities in 1999 and 25% (1 of 4) in 2000 occurred within the first six months of life. 0-6 month calf survival was 20% lower in 1999 (0.75) than in 2000 (0.94).

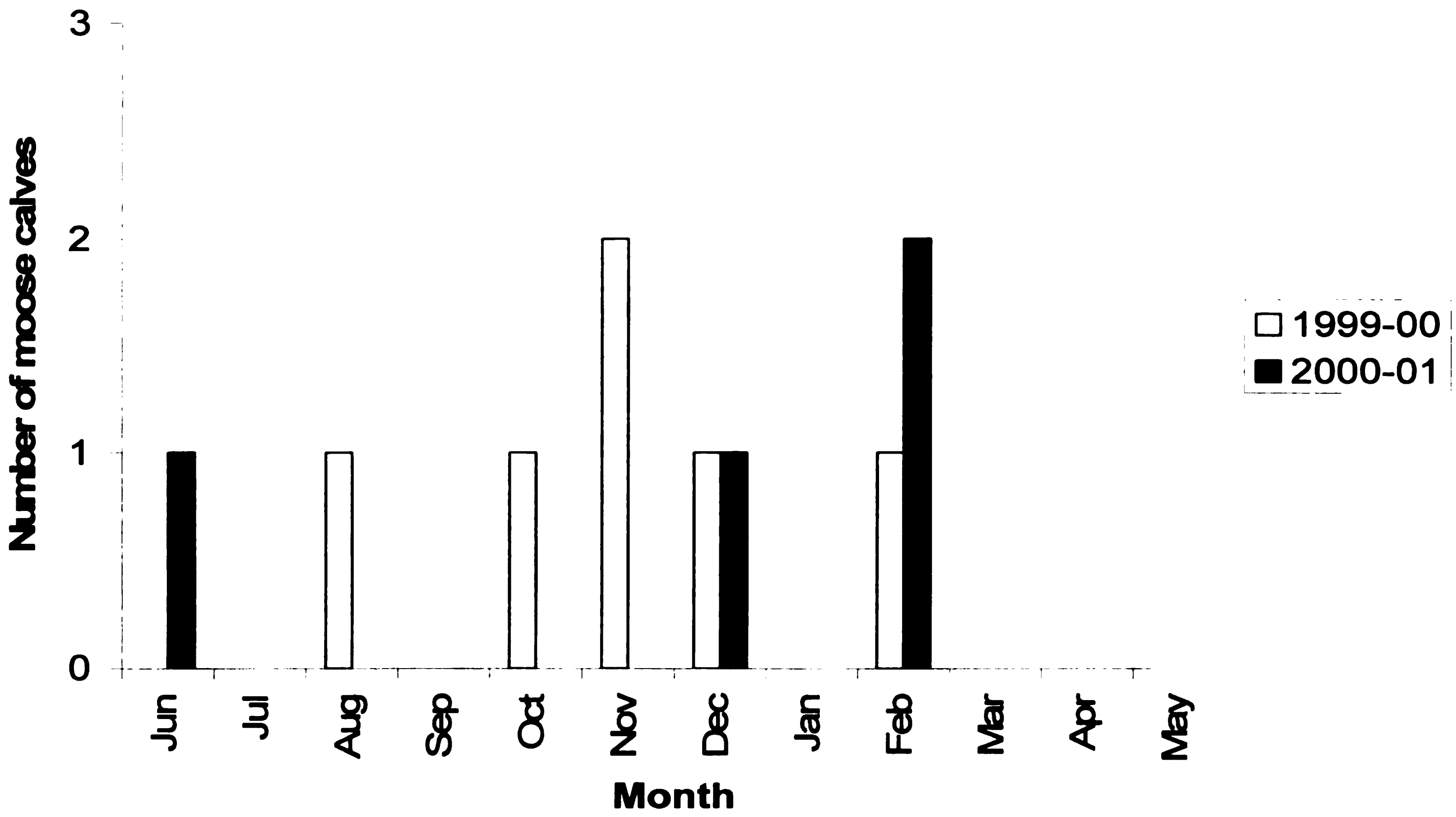

Figure 8. Number of radio-tagged and un-tagged calf moose deaths by month in the western Upper Peninsula of Michigan from 1 June 1999 - 31 May 2001

Calves 6-12 months of age

Thirty-three percent (2 of 6) of calf mortalities in 1999 and 75% (3 of 4) in 2000 occurred between 6 and 12 months of age. 6-12 month calf survival was 1% higher in 1999 (0.84) than in 2000 (0.83).

Mortalities

Moose died of various causes (Table 4). Only one moose, a yearling male (No. 106) was struck and killed by a motor vehicle during the study. All other moose died of natural causes or accidents. The 2 accidents merit further description. One yearling male (No. 114) died from stress and shock after breaking through ice at the edge of a pond and being unable to get out of the hole he created. Evidence at the site indicated that wolves had scavenged the carcass, but it could not be determined if they had actually killed him. A bull (No. 74) also died from stress and shock after becoming mired in a mud hole. The carcass of this moose was found mostly intact, claw marks on his back and rump indicated that he was attacked by a black bear post-mortum.

Only 1 moose, a yearling female (No. 160) was confirmed as being killed by wolves during the study. When captured she was originally identified as a calf because of her size relative to other calves previously radio-tagged. However, upon her death, aging by counting cementum annuli revealed that she was an extremely small yearling perhaps stunted by her ailment (see Table 4). In addition, capture stress may have contributed to her death.

Three moose were verified as having died from complications related to cerebrospinal nematodiasis (brain worm). Necropsies revealed that 47% percent

Table 4. Moose id, age at death, sex, femur marrow fat %, approximate date of death and diagnosed cause of death of radio-tagged moose studied during 1999-2001 in the western Upper Peninsula of Michigan.

Moose id	Age[a]	Sex	FMF%[b]	Death date	Diagnosis
74	7.50	M	79.07	18 Aug 2000	Stress, shock, trauma (possible predation), pericarditis, pneumonia, fascioloidiasis.
80	9.50	F	[c]73.91	30 Oct 1999	Cerebrospinal nematodiasis, hepatic abscess.
86	Adult	F	[e]NR	26 Jun 2000	Pericarditis, pneumonia (old age).
102	4.00	F	83.92	9 Apr 2001	Stress, shock.
106	1.75	M	85.67	19 Sep 1999	Trauma, struck by vehicle.
107	2.00	M	NR	16 Nov 2000	No diagnosis.
110	1.75	F	47.12	31 Oct 2000	Pulmonary congestion, malnutrition, fascioloidiasis.
114	1.75	M	12.46	27 Mar 2000	Stress, shock, trauma (possible predation), hepatic abscess.
115	4.75	F	74.16	17 Dec 2000	Pulmonary congestion, malnutrition, fascioloidiasis.
119	2.50	F	61.42	11 Nov 1999	Suffocation (rumen aspiration), pulmonary congestion.
122	2.50	F	8.22	7 Jan 2000	Fascioloidiasis, malnutrition, ascites.
143	1.00	F	NR	30 Jun 2000	No diagnosis
[d]144	Calf	M	NR	3 Apr 2000	Fascioloidiasis, malnutrition, tick infestation.
145	Adult	F	NR	31 May 2000	Birthing complication, fascioloidiasis, pericarditis
153	2.00	M	19.91	28 Apr 2001	Cerebrospinal nematodiasis, malnutrition, fascioloidiasis.
[d]159	0.50	F	38.63	13 Feb 2000	Cerebrospinal nematodiasis.
160	1.75	F	81.01	1 Mar 2001	Predation, fascioloidiasis, tick infestation.

[a] Cementum annuli.
[b] Femur marrow fat % dry weight.
[c] Humerus and tibia.
[d] Captured alone; not included in calf survival analysis.
[e] Data not recorded.

(8 of 17) of moose that died during the study were parasitized by the large American liver fluke. Five moose with liver flukes were also malnourished

Movements

Home range size and dispersion

Twenty-two percent (4 of 18) of adult radio-tagged moose were seasonally migratory during 1999-00. Three moose moved between distinct winter and summer home ranges. One cow was relocated in the same general area from winter until late-spring, then moved to a separate, distinct summer-fall home range. During 2000-01, 38% percent (14 of 37) of adult radio-tagged moose were seasonally migratory. Thirteen moose migrated between winter and summer home ranges. Again, as in 1999-00, the same cow migrated between a distinct summer-fall and winter-summer home range.

Seventy-five percent (3) of migratory moose in 1999 and 64% (9) in 2000 had seasonal home ranges that did not overlap. The remaining 6 (1 in 1999, 5 in 2000) had adjacent seasonal home ranges that overlapped < 25% (Table 5). Migratory moose with adjacent seasonal home ranges moved an average of 6 km (range=2-10 km) between summer and winter ranges, whereas those with spatially separate seasonal home ranges moved an average of 14 km (range=4-26 km).

The median size of winter, summer and annual home ranges of migratory adult moose were 23, 39, and 53 km^2 respectively (Table 6). Seasonal home ranges of migratory adult moose did not differ between winter and summer (Mann-Whitney *U* test, Z_{MWU}=-1.5615, P=0.1184). All migratory adult moose

Table 5. Percentage of overlap and distance between summer and winter home ranges of migratory adult radio-tagged moose studied during 1999 - 2001 in the western Upper Peninsula of Michigan.

Year	Moose id	Sex	Home range type[a]	% overlap	distance (km)[b]	Arrival on summer range	Arrival on winter range
1999-00							
	78	M	S	0.00	14.69	19-May	29-Sep
	92	M	S	0.00	7.93	29-Jun	13-Jan
	115	F	S	0.00	25.41		
	118	F	A	15.42	2.37	15-May	17-Nov
2000-01							
	28	F	S	0.00	12.31	5-Jun	18-Oct
	92	M	S	0.00	9.83	19-Jun	1-Dec
	108	F	S	0.00	4.52	26-May	7-Dec
	111	F	S	0.00	13.05	19-May	9-Jan
	115	F	S	0.00	26.14		
	116	F	A	2.43	6.18	26-May	30-Oct
	120	F	A	20.40	5.97	10-May	1-Nov
	123	F	S	0.00	15.57	19-May	11-Nov
	127	M	A	7.12	6.25	25-May	9-Oct
	139	F	A	4.90	4.94	15-May	8-Nov
	150	F	A	0.43	9.75	25-May	2-Jan
	151	F	S	0.00	17.18	25-May	27-Sep
	155	F	S	0.00	4.35	24-Mar	2-Jan
	156	F	S	0.00	11.97	24-Mar	25-Jan

[a] S – Separate home range; A – Adjacent home range
[b] Straight-line between centers of summer and winter FK-25% utilization distributions (UD).

Table 6. Annual and seasonal home range sizes of resident and migratory adult radio-tagged moose studied during 1999-2001 in the western Upper Peninsula of Michigan.

			95% fixed kernel				100% minimum convex polygon			
Home range type	No. moose	No. locations	Mean (km^2)	Median (km^2)	SE	Range	Mean (km^2)	Median (km^2)	SE	Range
Annual										
Migratory	18	20–30	63	53	7.12	20–122	33	32	4.53	10–91
Resident	37	19–34	43	41	3.49	14–99	30	31	2.22	10–65
$\bar{x}$ or total	55	19–34	49	44	3.5	14–122	31	31	2.09	10–91
Summer										
Migratory	16	11–24	44	39	6.04	9–98	26	20	4.15	3–2
Resident	44	11–24	41	36	3.84	4–115	20	20	1.97	6–63
$\bar{x}$ or total	60	11–24	42	37	3.22	4–115	23	20	1.90	3–72
Winter										
Migratory	8	10–15	27	23	7.58	3–64	12	8	3.28	2–28
Resident	20	9–15	20	12	3.92	1–57	9	7	1.84	1–30
$\bar{x}$ or total	28	9–15	22	15	3.52	1–64	10	8	1.59	1–30

were found on their summer ranges by the end of June each year. The earliest date a migratory moose was detected on its summer range was 3 May, the latest 19 June. Seventy-seven percent (17 of 22) of migratory adults had moved to their winter range by early December each year. The earliest date a migratory moose was found on its winter range was 27 September and the latest date 7 December. These dates do not include 3 cows that were not found on their 2000-01 winter range until early January. However, because these animals were not relocated in December it is possible that they had migrated earlier than was detected.

In addition, a bull and a cow were not found on their winter range until 13 January and 25 January, respectively. The bull made sporadic, relatively long distance movements ($\bar{x}$ = 5.22 km) between successive relocations during the autumn and early winter before moving to his winter home range. Prior to moving to her winter home range the cow established a distinct autumn range (16 August to 19 December, 2000-01).

The lone cow with atypical migratory behavior was found on her 15-km^2 summer-fall range from 13 July to 11 October in 1999-00. In 2000-01 she was found in the same, but smaller area (10-km^2) from 4 August to 9 October. In 1999-00 she was located on her winter-summer range (43 km^2) from 28 January to 20 July and in 2000-01 from 1 November until her death on approximately 20 December.

The remaining 37 adult radio-tagged moose were classified as resident animals. When winter and summer home ranges of resident moose were delineated, they overlapped >75%. Resident adult moose had median winter, summer, and annual home ranges of 12, 36, and 41 km^2 respectively (Table 6). Resident adult moose had significantly larger median summer home ranges than median winter home ranges (Z_{MWU}=-3.4255, P=0.0006). Annual median home ranges of migratory adult moose were larger (Z_{MWU}=2.4664, P=0.0136) than those of residents, whereas summer (Z_{MWU}=0.5266, P=0.5985) and winter (Z_{MWU}=0.7374, P=0.4609) home ranges did not differ between the groups.

Median home ranges of migratory and resident adult moose combined were 15 km^2 in winter, 37 km^2 in summer and 44 km^2 annually (Table 6). Median summer home ranges were significantly larger than median winter home ranges (Z_{MWU}=-3.7313, P=0.0002). There was no difference between median home ranges of cows and bulls (Z_{MWU}=0.0102, P=0.9919) (Table 7). Adult cows attended by calves had annual median home ranges that were 10% smaller than those of cows without calves (44 km vs. 49 km), but the difference was not significant (Z_{MWU}=0.6664, P=0.5052).

Median FK-95% adult annual home ranges were 42% larger than MCP-100% adult annual home ranges. Summer and winter median FK-95% home ranges of adults were 85% and 88% larger respectively, than summer and winter median MCP-100% home ranges of adults.

Annual median AD values (Table 8) did not differ between bulls and cows (Z_{MWU}=0.2166, P=0.8286), between yearling males and yearling females (Z_{MWU}=-0.6429, P=0.5203) or between cows with calves and cows without calves (Z_{MWU}=-0.1.4336, P=0.1517). However, at the 0.10 level of significance, annual

Table 7. Annual home range sizes of radio-tagged bull and cow moose studied during 1999-2001 in the western Upper Peninsula of Michigan.

			95% fixed kernel				100% minimum convex polygon			
Classification	No. moose	No. locations	Mean (km^2)	Median (km^2)	SE	Range	Mean (km^2)	Median (km^2)	SE	Range
Adults										
Bulls	12	19–24	47	43	5.97	22–80	31	34	3.12	10–44
All Cows	43		50	44	4.19	14–122	31	30	2.54	10–91
Cows w/ calves	29	21–34	48	44	5.19	14–115	29	23	2.88	10–65
Cows w/ out calves	11	20–28	51	49	6.01	25–96	32	31	2.77	17–44

Table 8. Annual and seasonal Euclidian (or linear) distance (AD) between pairs of relocations of adult and yearling radio-tagged moose studied during 1999-2001 in the western Upper Peninsula of Michigan.

Classification	No. moose	No. locations	Distance (km) Mean	Median	SE	Range
Adults						
Bulls	11	20 – 25	4.33	4.02	0.42	2.37 – 6.69
All Cows	45	20 – 34	4.05	3.72	0.47	1.89 – 14.51
Cows w/ calves	32	20 – 34	4.75	3.43	0.58	1.89 – 14.51
Cows w/ out calves	11	21 – 30	5.23	4.02	0.94	3.12 – 13.90
Yearlings						
Males	6	21 – 23	5.54	4.80	0.91	3.56 – 9.56
Females	5	20 – 24	7.74	3.95	3.91	3.05 – 23.30
Summer[a]						
Bulls	4	10 – 12	3.12	2.84	0.56	2.18 – 4.63
Cows	30	10 – 17	4.06	3.09	0.61	1.26 – 5.17
Yr. males	3	10 – 10	3.26	3.70	0.54	2.19 – 3.91
Yr. females	5	10 – 16	3.14	3.22	0.60	1.60 – 5.08
Fall[b]						
Cows	8	10 – 14	4.60	3.05	1.21	2.20 – 12.51
Winter[c]						
Cows	20	10 – 13	2.94	3.04	0.34	0.54 – 6.52

[a]Summer = May – August.
[b]Fall = September – December.
[c]Winter = January – April.

median AD of yearlings was greater than that of adults (Z_{MWU}=1.8646, P=0.0612). Adequate numbers of relocations (>9 per moose) were available to make statistical comparisons among seasonal AD values for radio-tagged cows only. Mean seasonal AD values indicated that the movements of cows were less dispersed during the winter ($\overline{x}$=2.94 km) than during the summer ($\overline{x}$=4.06 km) or fall ($\overline{x}$=4.60 km) (Table 8). However, the Kruskal-Wallace test detected no significant difference (χ^2_2=1.243, P=0.5372) among median seasonal AD values of cows.

Dispersal and home range development

Six radio-tagged moose permanently dispersed out of the core study area, 3 each in 1999-00 and 2000-01 (Table 9, Figure 9). Dispersers included 3 yearling males and 2 yearling females (see below), and 1 adult female (cow). The cow, 1 yearling male and both yearling females dispersed in April-June. The other 2 yearling males dispersed in January and September. The mean $\pm$SE linear distance dispersed was 80$\pm$16 km and ranged from 30 to 134 km. The average number of days a yearling moose wandered from the time a dispersal movement was detected until it ceased because the moose established a new home range, it died or dropped its radio-collar or the study ended, was 164 days (range=25-592). The estimated annual dispersal rate in 1999 ($\hat{D}$=0.068) was 26% greater than in 2000 ($\hat{D}$=0.054) (Table 10).

Two moose that dispersed, a yearling male (No. 104, see details below) and a cow (No. 185, radio-tagged 13 February 2001) established new home ranges in northeastern Wisconsin (Figure 9). During a 16-day period (8 April-24 April 2001) the cow moved 64 km in a southwesterly direction to an area in Forest County Wisconsin where she permanently settled (Figure 10).

In addition, a cow (No. 102) captured as a yearling on 29 January 1999 permanently shifted her range within the core study area (Figure 11). Following capture she established a home range of 23 km^2 that was 3-4 km southwest of the town of Nestoria which she occupied through March 2000. On 28 April 2000

Table 9. Radio-tagged moose that dispersed out of the core study area during 1999-2001 in the western Upper Peninsula of Michigan.

Moose id	Sex	Age	Date dispersal initiated[a]	Dispersal distance (km)[b]	Dispersal distance (km)[c]	Days[d]	Fate
106	M	Y	28-Jun-1999	93	145	73	Died 9-Sep-1999
104	M	Y	15-Sep-1999	134	302	592	Home range in Wisconsin
131	M	Y	4-Jan-2000	114	157	73	Last relocated 5-Jun-2001
105	F	Y	24-Apr-2000	47	46	25	Dropped collar 14-Jul-2000
185	F	A	16-Apr-2001	64	64	8	Home range in Wisconsin
134	F	Y	3-May-2001	30	31	16	Last relocated 29-Jun-2001

[a] Median date between date last found on natal or former annual home range and date first found after dispersal.
[b] Straight-line between centers of FK 25% utilization distribution (UD) of pre- and post-dispersal home ranges or between pre- and post-dispersal relocations.
[c] Includes intervening relocations.
[d] Until establishment of new home range, dropped radio-collar, death or study ended.

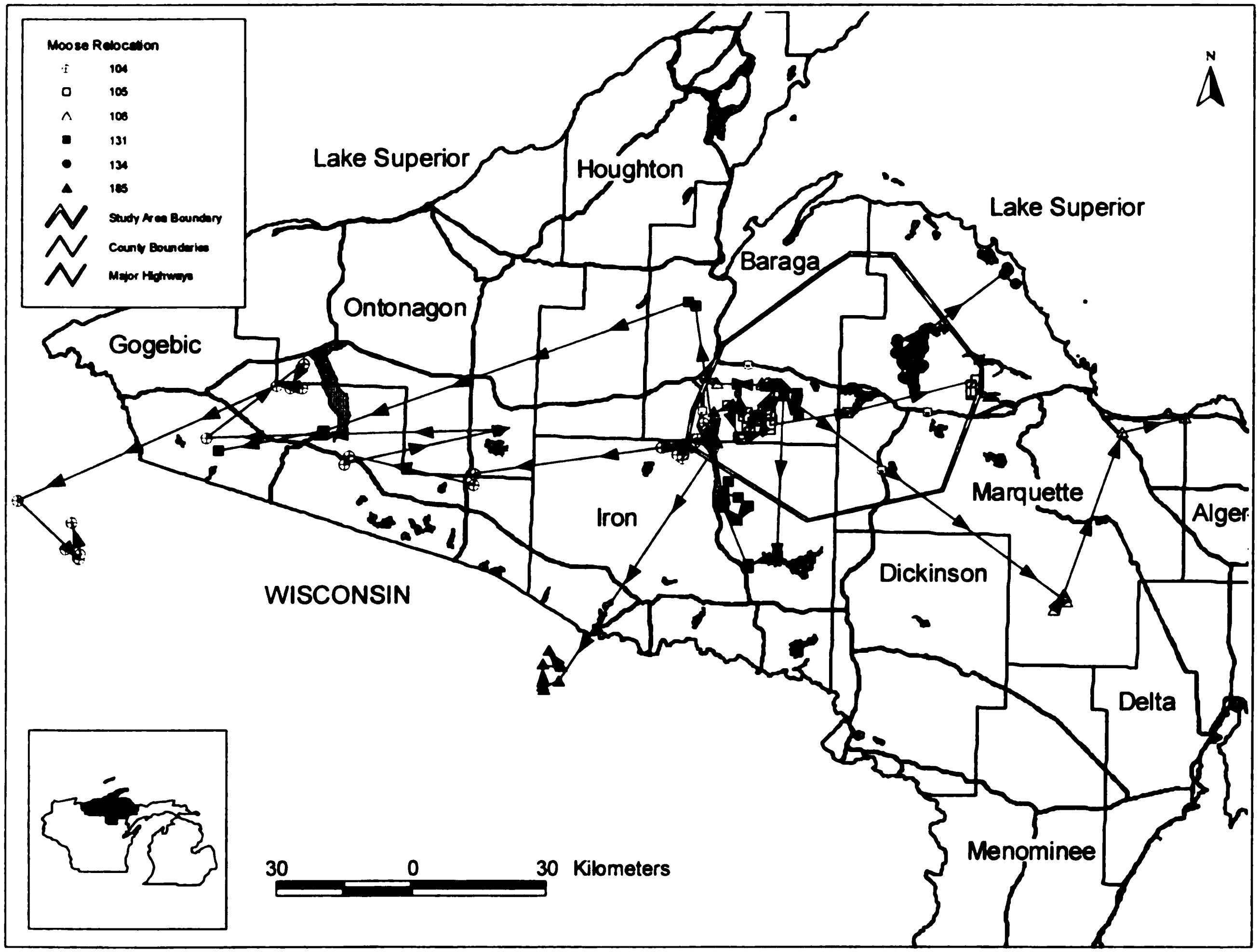

Figure 9. Relocations and movements of six radio-tagged moose that dispersed out of the core study area during 1999-2001 in the western Upper Peninsula of Michigan.

Table 10. Annual dispersal rates of radio-tagged adult and yearling moose studied during 1999-2001 in the western Upper Peninsula of Michigan.

Year	Rate	SE	No. moose	No. months	No. dispersing	95% LCI	95% UCI
1999	0.068	0.0017	42	514	3	0.000*	0.139
2000	0.054	0.0012	56	657	3	0.000*	0.112

[a]Dispersal rates calculated using the Mayfiled estimator (Mayfield 1961,1975).
*Lower interval truncated at 0.00.

she was relocated 5 km south of Shank Lake in Iron County. Approximately 1-month later (25 May) she was relocated 3-km northeast of Van Riper State Park, 35 km to the northeast of her previous location. Four days later (29 May) she was found18 km further east. Thereafter, she established a new home range of 21 km^2 several kilometers west of the Dead River Storage Basin by 20 June 2000. She occupied this home range until her death on 25 May 2001.

Twenty-six calves - the offspring of 23 radio-tagged cows - were radio-tagged during captures in 1999, 2000, and 2001. The areas occupied and movements after cow-calf separation of 11 (7 males, 4 females) of these moose (henceforth referred to as yearlings) for which an adequate number of relocations were available, were examined. In addition, the movements of 2 yearling males who wandered extensively prior to permanently dispersing were investigated.

The mean $\pm$ SE age at which a calf became independent of its cow was 11 $\pm$ 0.25 months and ranged from 7.5 to 13.0 months. Calves (n=5) of cows that were barren the next calving season remained with their cow 11-days longer than calves (n=20) who's cow gave birth the following season. The median date of

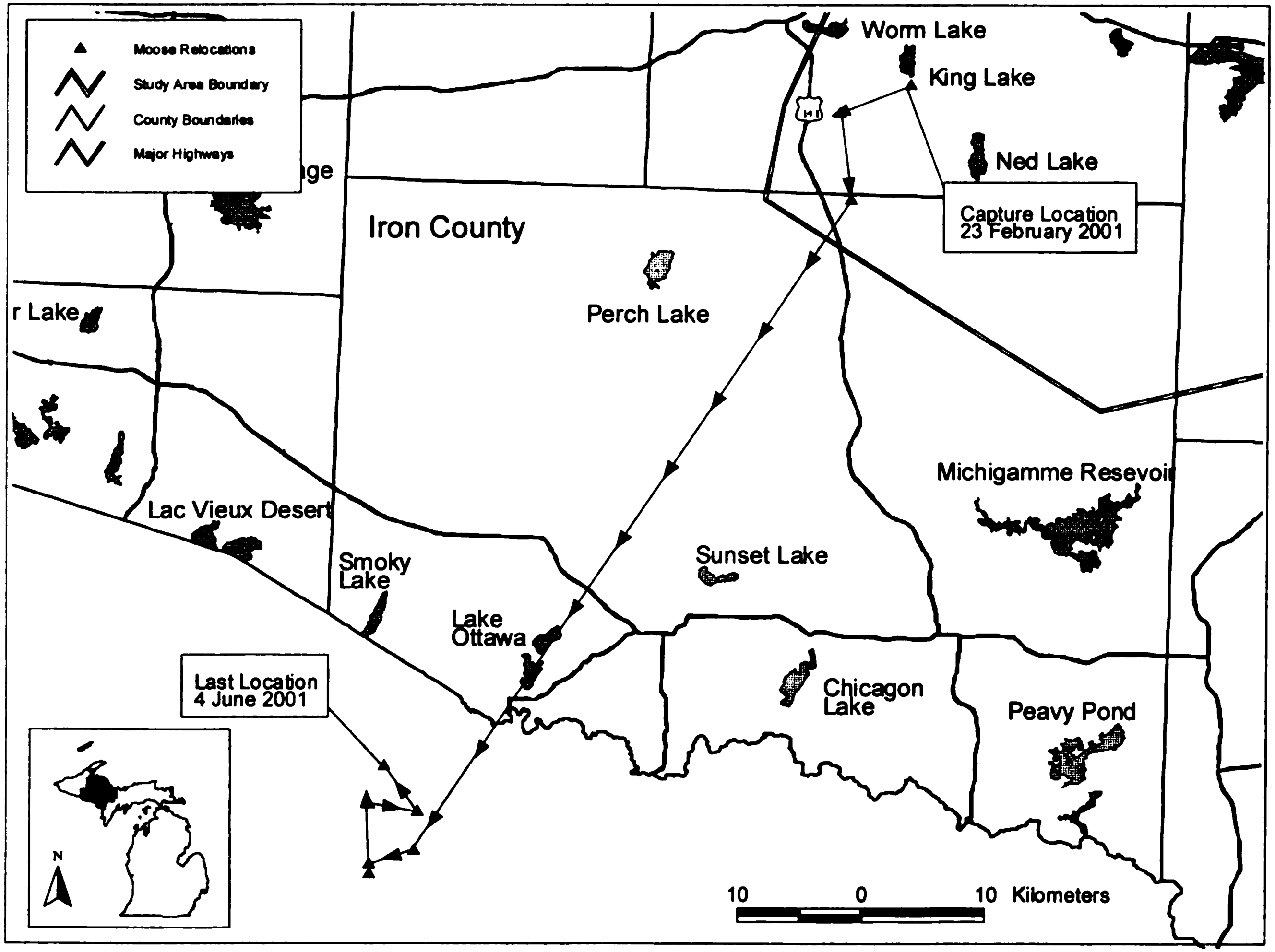

Figure 10. Relocations and movements of radio-tagged cow moose (No. 185) during 2001 in the western Upper Peninsula of Michigan.

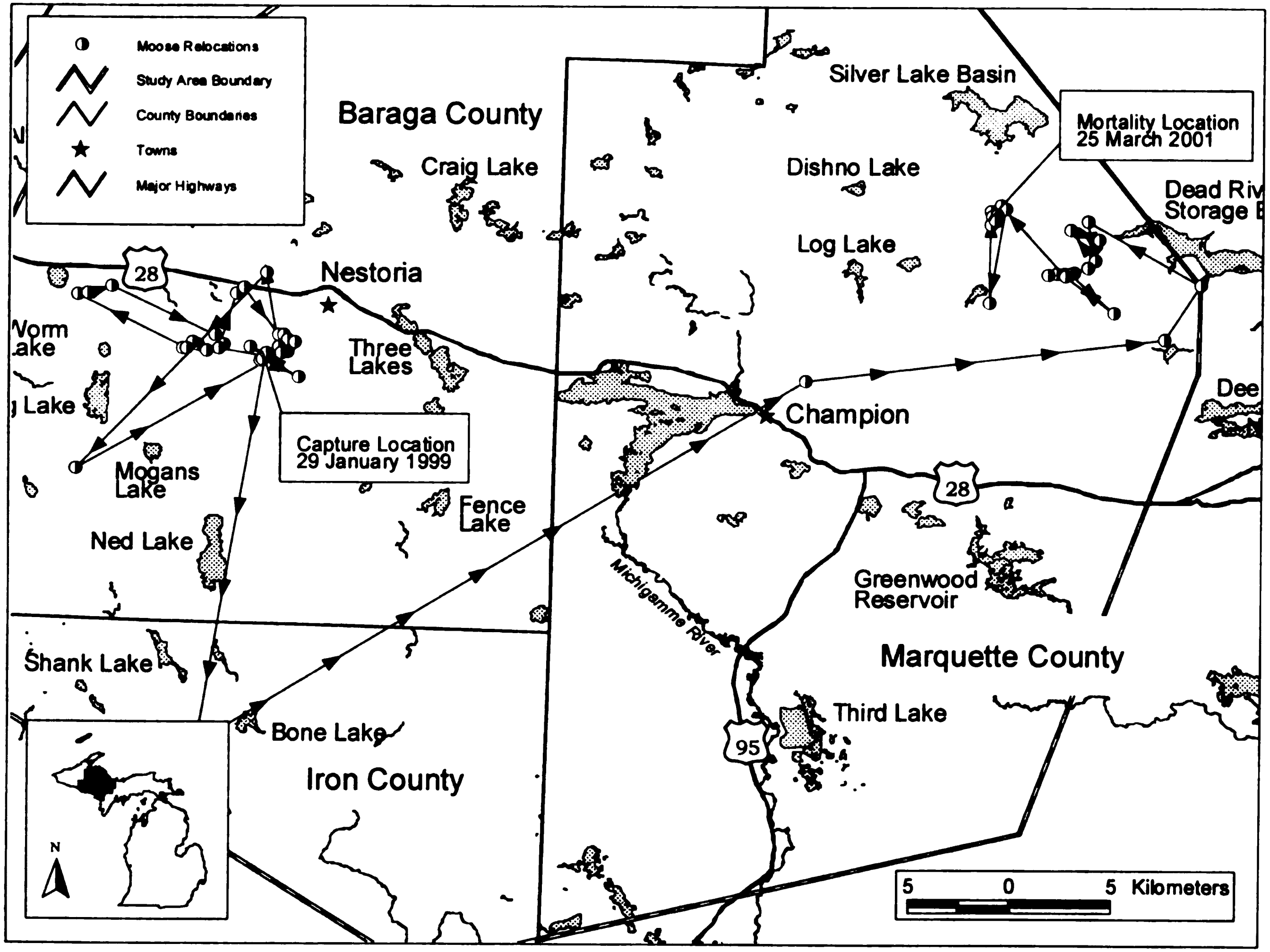

Figure 11. Relocations and movements of radio-tagged cow moose (No. 102) during 1999-2001 in the western Upper Peninsula of Michigan

separation for the former group was 21 May, whereas for the latter group it was 1 April.

During their first one and a half years following independence, yearling moose exhibited three movement patterns, they either (A) permanently dispersed out of the core study area over 1 to 16 months, (B) occupied areas that partially overlapped their cow's summer and/or winter home range for periods of 9 to 13 months or (C) occupied areas in the summer that partially overlapped their cow's summer home range but moved to completely separate areas in the winter.

Two yearlings (1 male, 1 female) captured in 1999 and 2 (1 male, 1 female) captured in 2000 permanently dispersed after separating from their dams (pattern A). Also, a yearling male (No. 106), captured alone on 29 January 1999 permanently dispersed. Three yearlings occupied temporary home ranges that were completely separate from their cow's home range prior to dispersing. Yearling male, No. 104 (radio-tagged 30 January 1999) occupied a 17 km^2 home range, yearling female, No. 105 (radio-tagged 30 January 1999) a 39 km^2 home range and yearling female, No. 134 (radio-tagged 20 January 2000) a 54 km^2 home range.

No. 104 occupied his temporary home range through early September of 1999, then wandered in a westerly direction (Figure 12). He was next found near Lake Gogebic where he remained until 6 September 2000. Then, from mid-September 2000 until late-March 2001 he moved 82 km in a southwesterly direction. In late-April 2001 he appeared to establish a home range northwest of Mercer, Wisconsin. Taken in whole, over a 242 day period (7 September 2000-6

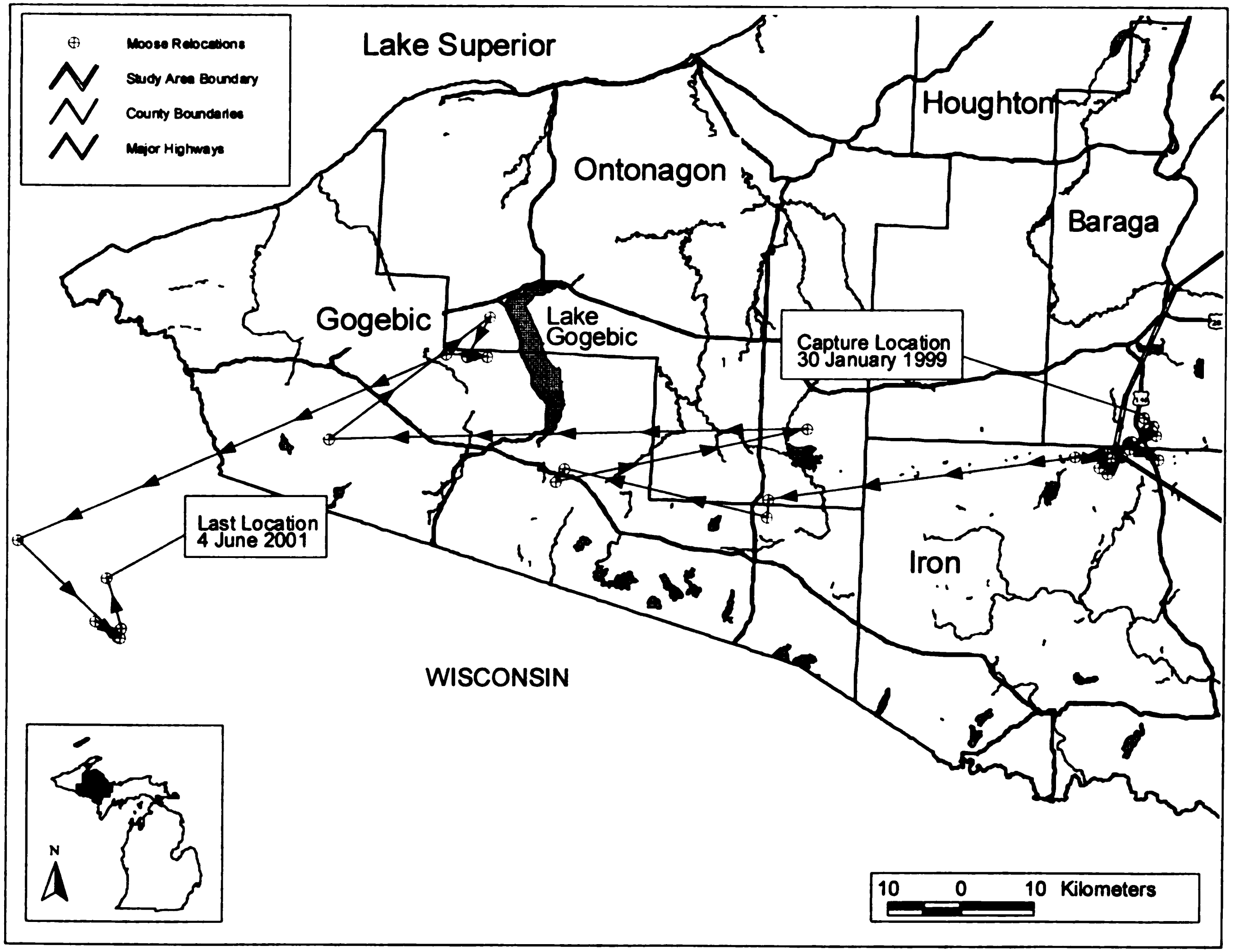

Figure 12. Relocations and movements of radio-tagged yearling male moose (No. 104) during 1999-2001 in the western Upper Peninsula of Michigan.

May 2001), No. 104 covered a distance of at least 205 km.

Following separation from her cow in late February 1999, No. 105 was found on her temporary home range through March 1999. Thereafter, over a 2-month period she moved 48 km in an easterly direction (Figure 13). Unfortunately, any further monitoring of this moose ended when her radio-collar was recovered on 14 July 2000.

From the date she was first relocated alone on 25 may 2000, until her signal was temporarily lost after 18 April 2001, No. 134 wandered throughout her temporary home range. On 15 May 2001 we picked-up her signal and relocated her 5-km southeast of Lake Independence, 31-km to the northeast of her prior location (Figure 14). When last relocated (29 June 2001) she had moved 3-4 km to the southeast.

The other 2 males (Nos. 106 and 131) that exhibited pattern A movements wandered over large areas (>250 km^2) before eventually dispersing. After roaming nomadically for 4 months, No. 106 was struck and killed on 19 September 1999 by a westbound vehicle on state route M-28, 0.4 km west of the Sand River (Figure 15). Eight days after being captured on 20 January 2000, No. 131 was found alone, >7 km from where his cow (No. 123) was relocated. Following long movements both south (36 km) and north-northwest (60 km) of his capture location over a 9-month period, his signal was lost in late-October 2000. Five months later he was found 85 km southwest of his previous location. He was last relocated on 5 June 2001 near Lake Gogebic (Figure 16).

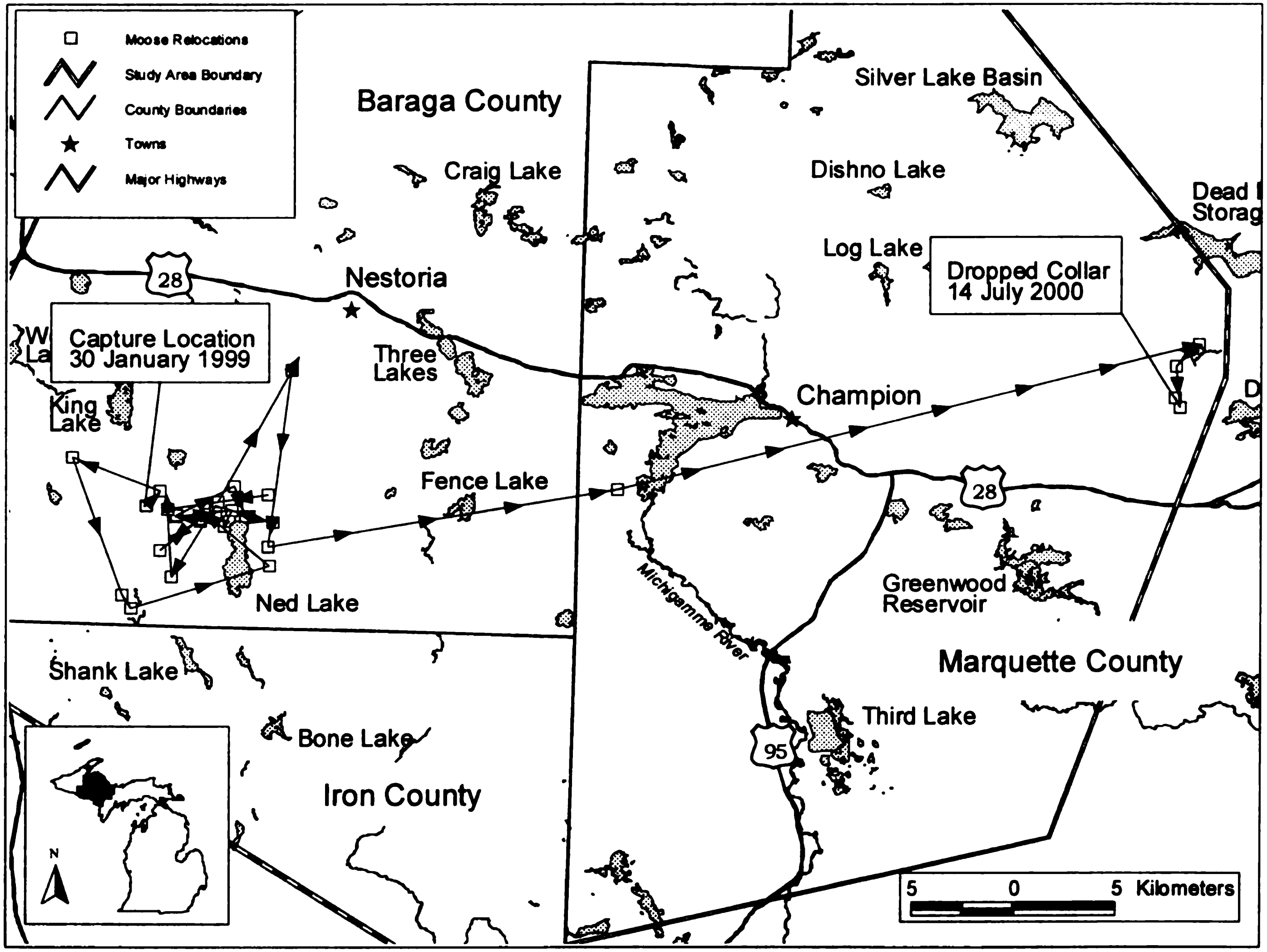

Figure 13. Relocations and movements of radio-tagged yearling female moose (No. 105) during 1999-2000 in the western Upper Peninsula of Michigan.

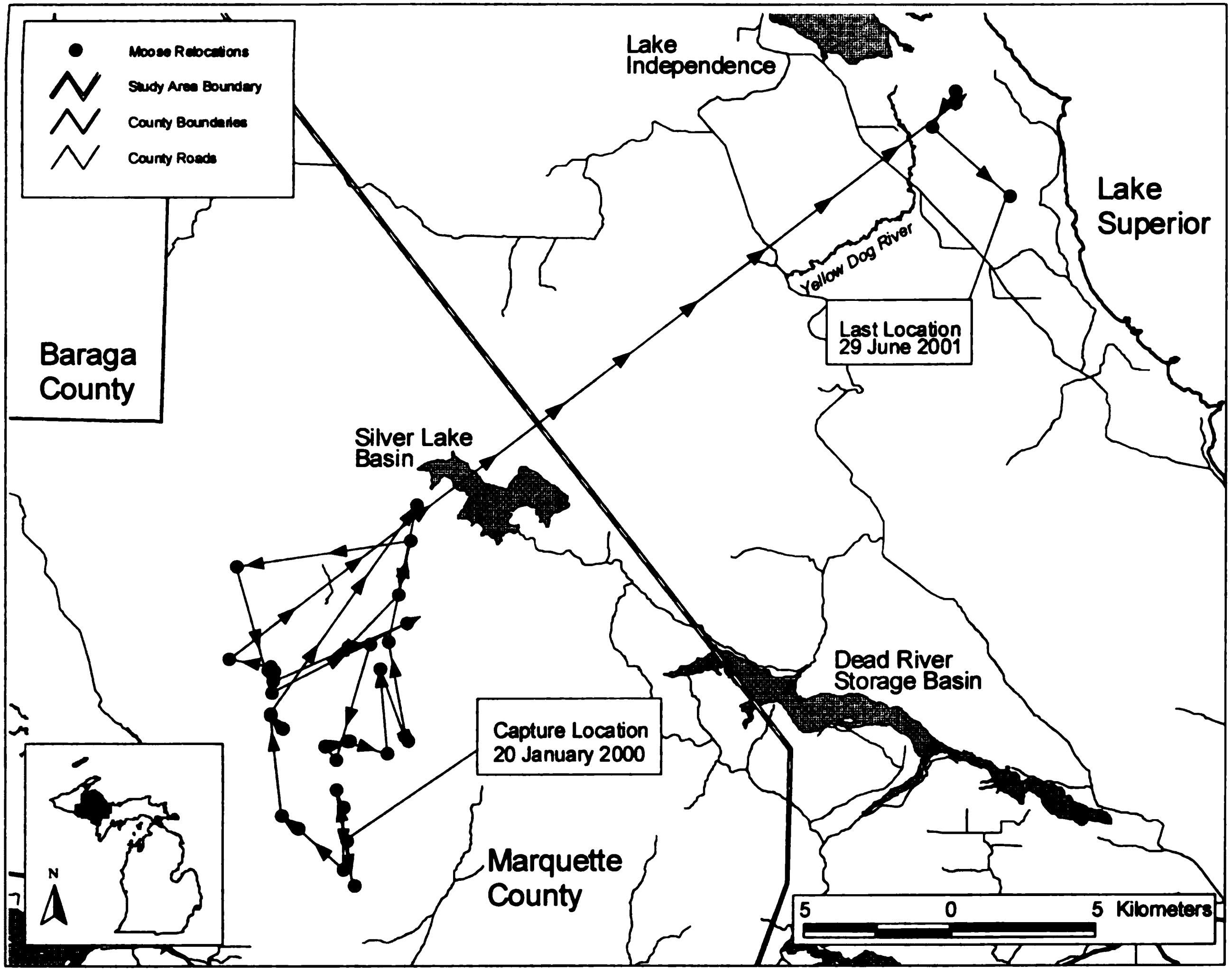

Figure 14. Relocations and movements of radio-tagged yearling female moose (No. 134) during 2000-2001 in the western Upper Peninsula of Michigan.

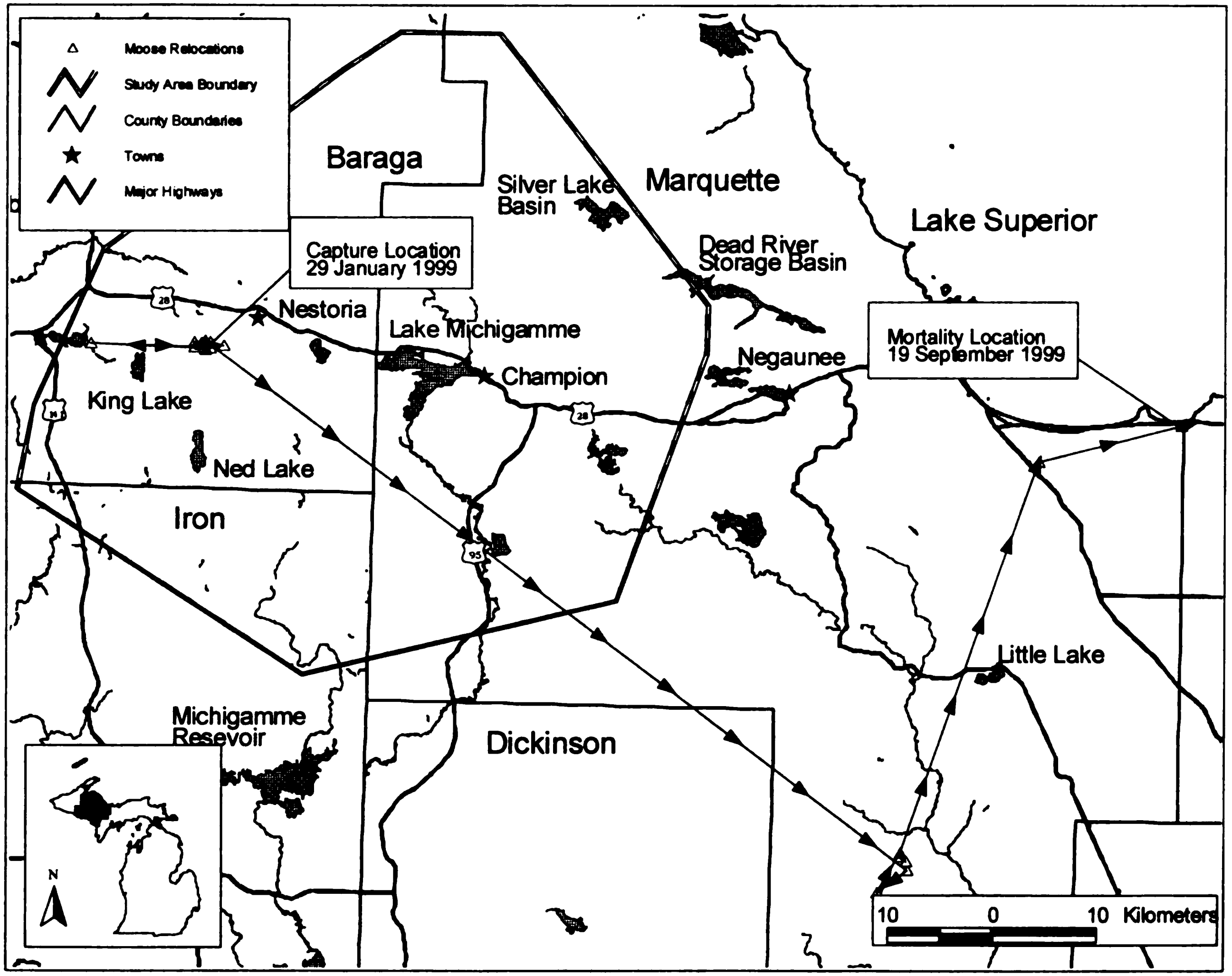

Figure 15. Relocations and movements of radio-tagged yearling male moose (No. 106) during 1999-2000 in the western Upper Peninsula of Michigan.

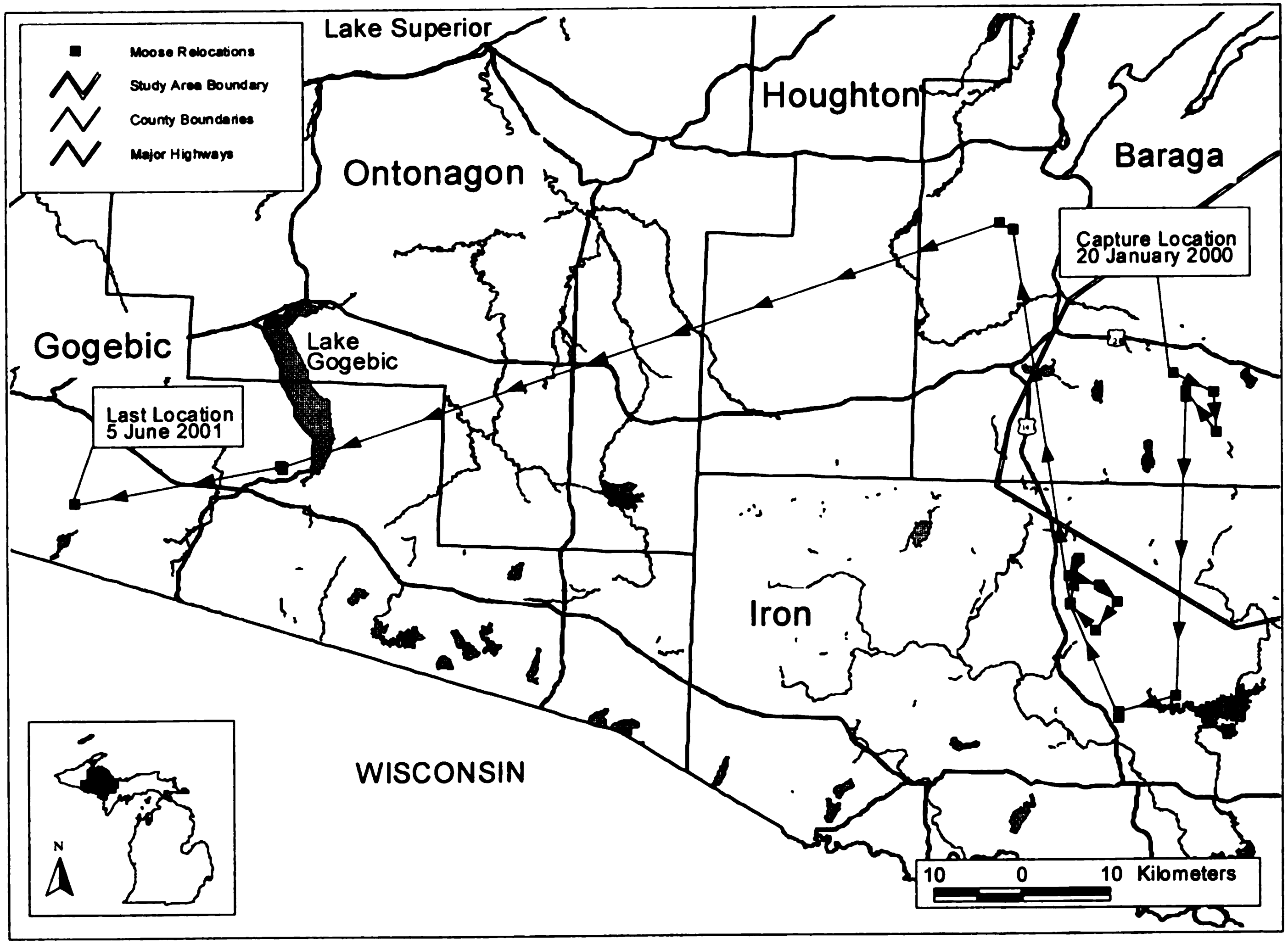

Figure 16. Relocations and movements of radio-tagged yearling male moose (No. 131) during 1999-2000 in the western Upper Peninsula of Michigan.

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Six yearlings (4 males, 2 females) exhibited pattern B movements after separation from their cows. Four were offspring of resident cows and 2 were offspring of seasonally migratory cows. The mean $\pm$ SE and median areas occupied by these yearlings was 57 $\pm$ 13 and 42 km^2 (range=30-108 km). There was a 47% (range=31-72%) overlap of the area occupied by offspring of resident cows and their cow's annual home range. The distance between concentrated areas of activity (i.e., the FK-25% UD) of a resident cow's seasonal home ranges and the area occupied by her offspring averaged 4 km in the summer and 7 km in the winter. One yearling male (No. 107), the offspring of a cow that migrated between summer and winter home ranges occupied an area that overlapped 27% of his cow's summer home range. His area of concentrated activity was 11 km from that of his cows' when she was on her summer home range and was 13 km after she had migrated to her winter home range. The remaining yearling male (No. 114) was the offspring of the cow (No. 115) that migrated between summer-fall and winter-summer home ranges. He occupied an area of 24 km^2 between 26 April 1999-31 March 2000 that included 18% of his cow's winter-summer home range. The linear distance between the cow's center of activity and that of her yearling was 6 km when she occupied her winter-summer home range and was 29 km when she occupied her summer-fall home range. On two separate occasions, No. 115 made exploratory movements outside the area he occupied. On 13 September 1999 he was located 16 km to the northeast, within 4 days he had returned. The second movement began in mid-October 1999 and lasted until late-January the following year. The linear round-trip distance he moved during this period was 50 km.

Three yearling males (Nos. 138, 148 and 153) exhibited pattern C movements after separation. Between late-May and mid-September No. 138 occupied an area of 27 km^2, No. 148 an area of 10 km^2 and No. 153 an area of 15 km^2. The overlap of these areas with their cow's summer home range was 20% for No. 138, 8% for No. 148 and 10% for No. 153. The distance between the activity centers of these areas and that of their cow's summer home range varied from 1 to 3 km. In late-September all 3 moved to areas that were completely separate from the winter home range of their cow. No. 138 occupied an area of 12 km^2 that was 50 km distant, No. 148, an area of 9 km^2 that was 41 km distant and No. 153 an area of 20 km^2 that was 18 km distant from their cow's winter home range. All 3 remained on their winter range until late-April. No. 153 died on 28 April 2001, No. 138 was last relocated 16 km south of his winter range and No. 148, 28-km southwest of his winter range.

Reproduction

Pregnancy determination

Relative to the 84% average pregnancy rate of adult moose in North America (Boer 1992), pregnancy rates in the western Upper Peninsula of Michigan were moderate each year: 78% (n=14) in 1999, 70% (n=19) in 2000, and 74% (n= 31) in 2001.

Seventy percent (24 of 34) of cows from which blood samples were collected in 1999, 2000, and 2001 had detectable PSPB levels indicating pregnancy. Pooled 2000-2001 mean ± SE and median PSPB values were 411.05 ± 69.38 and 387.30 ng/mL respectively (Table11).

Table 11. Pregnancy specific protein B (PSPB) concentration (ng/mL) in blood serum collected in winter from radio-tagged cow moose in the western Upper Peninsula of Michigan, 2000-2001. All cows with detectable levels of PSPB were considered to be pregnant.

Year	$\bar{x}$	SE	Median	Min	*Max*	*n*
2000	297.01	51.38	261.55	76.70	553.70	8
2001	541.39	123.43	475.40	76.50	996.60	7
Pooled	411.05	69.38	387.30	76.50	996.60	15

Due to the small number of twin calves produced by cows for which we had blood samples, we did not attempt to correlate PSPB to calf production. Eighty-nine percent (8 of 9) of cows that had positive PSPB results in the winter of 1999 were seen with calves in the spring. The lone cow not seen with a calf was missing at the time calf checks were conducted. Three cows that had negative PSPB results in the winter of 1999 did not reproduce calves. In 2000, 83% (5 of 6) of cows that had positive PSPB results were believed to have reproduced. We were unable to assess the calving status of one cow until mid-July and it is possible that she had given birth and that her calf had subsequently died. PSPB results in winter 2001 diagnosed 70% (7 of 10) of captured cows as being pregnant, however only 3 pregnant cows were seen with calves in the spring. Serum and fecal progesterone levels also indicated that these animals were pregnant. It is difficult to believe that all 3 testing methods would result in false-positive results. Although these cows were approached multiple times during the calving season it is possible that we missed the calf (calves), (1)

Table 12. Progesterone concentration (ng/mL) in blood serum collected in winter from radio-tagged cow moose in the western Upper Peninsula of Michigan, 1999-2001. The 95% Upper tolerance limit (95% UTL) or dividing serum progesterone level between pregnant and non-pregnant cows was 1.68 ng/mL.

	Pregnant moose					Non-Pregnant moose				
Year	$\bar{x}$	SE	Median	Min	*N*	$\bar{x}$	SE	Median	Max	*n*
1999	5.74	0.97	4.82	2.47	9	0.99	0.45	1.26	1.60	3
2000	4.44	0.21	4.50	3.55	8	0.18	0.08	0.18	0.33	3
2001	3.16	0.20	3.47	2.23	7	0.65	0.16	0.56	0.96	3
Pooled	4.56	0.42	4.28	2.23	24	0.61	0.18	0.43	1.6	9

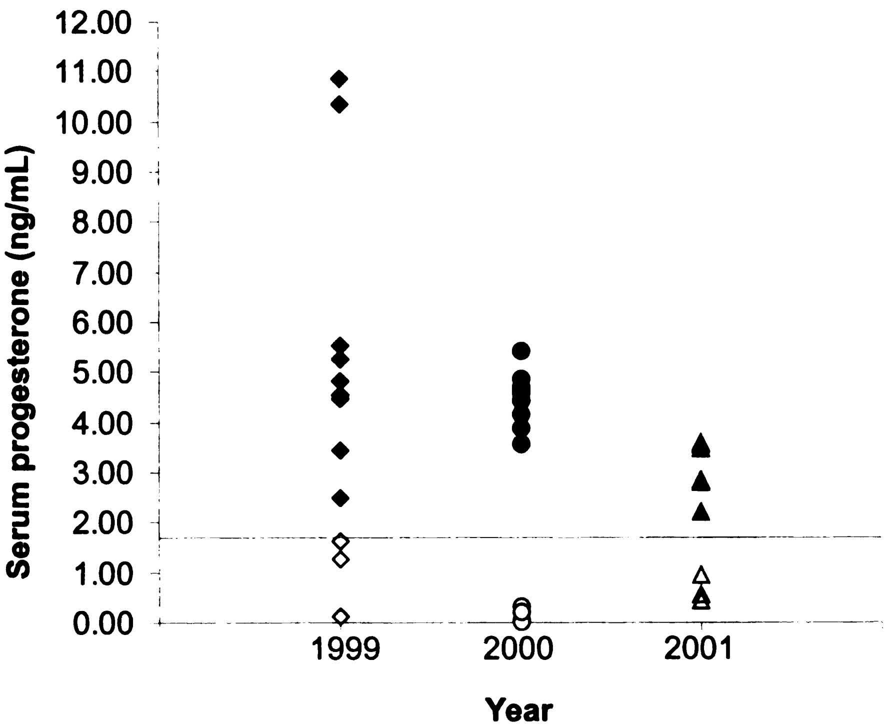

Figure 17. Progesterone concentration in blood serum collected in winter from radio-tagged moose in the western Upper Peninsula of Michigan, 1999-2001. Each symbol represents the serum progesterone concentration of a single moose. The 95% upper tolerance limit (95% UTL) or dividing serum progesterone level between non-pregnant (◇, ○, △) and pregnant (◆, ●, ▲) cows was 1.68 ng/mL.

because the calf (calves) died shortly after birth or, (2) the calf (calves) died sometime in the interval between cow sightings.

Useable blood serum samples were obtained from 33 cows. Blood serum progesterone concentrations fell into fairly distinct pregnant and non-pregnant groups each year (Figure 17). Mean $\pm$SE and median values pooled across years were 4.56 $\pm$0.42 and 4.28 ng/mL for pregnant cows and 0.61 $\pm$0.18 and 0.43 ng/mL for non-pregnant cows (Table 12). As expected, blood serum progesterone concentrations of pregnant cows were significantly different from those of non-pregnant cows ($Z=-4.3454$, $P<0.0001$) (Mann-Whitney *U* test). The 95% UTL of serum progesterone concentration for non-pregnant cows was 1.68 ng/mL. Using the 95% UTL, the pregnancy status of all cows would have been correctly identified (Figure 17).

Between January 1999 and May 2001, we collected 119 fecal samples from 36 radio-tagged cows. Multiple samples were collected from 16 cows in the winter of 2000 ($\overline{x}$=2.19 $\pm$0.100) and from 19 cows in the winter of 2001 ($\overline{x}$=2.05 $\pm$0.05). The results of 3 fecal samples with very low progesterone levels (<1.4 μg/g), 1 of 2 samples collected from 3 different cows, were not included in the analysis. They were removed because the cows were seen with calves during spring calf checks, results from other fecal samples indicated that the cows were pregnant, and the origin of the samples, when collected in the winter, was in doubt. Fecal progesterone concentrations also fell into fairly distinct pregnant and non-pregnant groups each year, although the results were not unequivocal (Figure 18). Pooled across years, the mean$\pm$SE and median values for

Table 13. Progesterone concentration (μg/g) in fecal material collected in winter from radio-tagged cow moose in the western Upper Peninsula of Michigan, 1999-2001. The 95% Upper tolerance limit (95% UTL) or dividing fecal progesterone level between pregnant and non-pregnant cows was 5.17 μg/g.

	Pregnant moose					Non-Pregnant moose				
Year	$\bar{X}$	SE	Median	Min	*N*	$\bar{X}$	SE	Median	Max	*n*
1999	6.07	1.26	5.36	1.13	9	0.97	0.35	1.12	1.50	3
2000	11.82	0.68	10.45	4.29	36	3.23	0.45	3.10	5.9	12
2001	22.30	1.40	22.89	1.35	42	1.65	0.44	1.27	4.22	11
Pooled	16.29	0.98	14.46	1.13	87	2.30	0.32	2.66	5.90	26

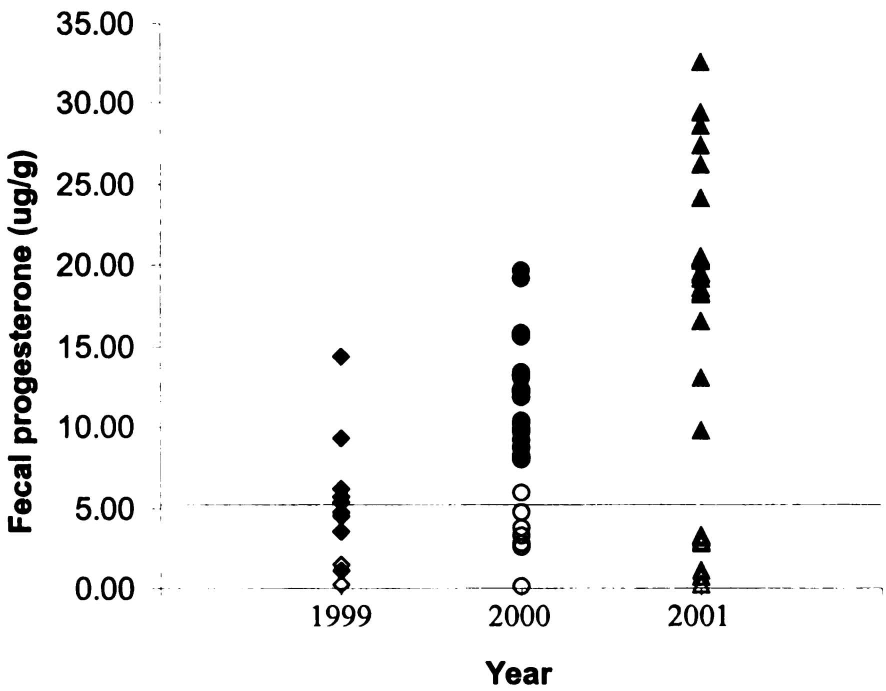

Figure 18. Progesterone concentration in fecal material collected in winter from radio-tagged cow moose in the western Upper Peninsula of Michigan, 1999-2001. Each symbol represents the mean fecal progesterone concentration of a single moose. The 95% Upper tolerance limit (95% UTL) or dividing fecal progesterone level between non-pregnant (◇, ○, △) and pregnant (◆, ●, ▲) cows was 5.17 μg/g.

pregnant cows were 16.29±0.98 and 14.46 μg/g, whereas for non-pregnant cows the values were 2.30±0.32 and 2.66 μg/g (Table 13). As expected, fecal progesterone concentrations of pregnant cows were significantly different from those of non-pregnant cows ($Z=-7.1730$, $P<0.0001$). The 95% UTL of fecal progesterone concentration for non-pregnant cows was 5.17 μg/g. Ninety-two percent (44 of 48) of pregnant cows and 94% (17 of 18) of non-pregnant cows would have been correctly identified using the fecal 95% UTL. The 4 false-positive fecal results were from single samples collected from cows during capture in 1999, however PSPB and serum progesterone levels correctly identified them as being pregnant.

Ten radio-tagged yearling females survived long enough to possibly reproduce. Only one (No. 109) gave birth to a single calf in 1999. Among the remaining 9, 3 had negative pregnancy test results, 3 were seen alone during spring natality checks, 2 were unknown as regards to calving, and 1 dispersed the summer of her second year of life. The maximum yearling pregnancy rate, if we include the 2 moose with unknown calving status, then would be only 30%.

Productivity

<u>Natality and Recruitment</u>

The method in which parturition was determined did not lend itself well to estimating the birth dates of calves. As expected, 90% of calves were seen between 15 May and 30 June each spring. The earliest observation of a radio-tagged cow with calves was 21 May in 1999, 24 May in 2000, and 15 May in 2001. In spring 1999, pregnant cows (n=14, 78%) were approached on the ground an average of 1.86 times before their calving status was determined. Two pregnant cows (1 per flight) were observed with offspring during aerial relocation flights on 10 June and 26 June 1999. In spring 2000, pregnant cows (n=20, 71%) were approached on the ground an average of 1.50 times before their calving status was determined. Three pregnant cows (1 per flight) were seen with calves during aerial relocation flights on 25 May, 27 May, and 29 June 2000. In addition, 4 radio-tagged cows classified as non-pregnant were each seen alone in the spring of 2000 during separate aerial relocation flights. In spring 2001, pregnant cows (n=31, 74%) were approached an average of 1.71 times before their calving status was determined. No pregnant cows attended by calves were seen from the air in 2001.

Among cows that tested positive for pregnancy, 100% in 1999 (n=8), 94% in 2000 (n=17), and 76% in 2001 (n=29) were observed with at least 1 calf in the spring. Radio-tagged cows produced 19 calves in 1999, 20 calves in 2000, and 29 calves in 2001. Post-calving calf:cow ratios decreased each year: 1.06 in 1999, 0.71 in 2000, and 0.69 in 2001. Frequency of twinning differed among years (Table 14, Figure 19). The highest rate, 36% occurring in 1999 when the fewest number of cows (n=18) were radio-tagged. The lowest rate was observed in 2000 when only 6% of cows that reproduced gave birth to twins. The rate increased 71% the next year when 21% of cows that gave birth had twins. Annually, twinning rates averaged approximately 19%. Calf:cow ratios decreased throughout the year due to the loss of a greater number of calves than cows. Between post-calving and pre-calving the following year, calf:cow ratios

Table 14. Annual reproductive parameters of radio-tagged cow moose studied during 1999-2001 in the western Upper Peninsula of Michigan.

Year	Total no. cows	% cows pregnant	No. calves produced	% twins	Spring calf : cow	Fall calf : cow
1999	18	78	19	36	1.06 : 1	0.76 : 1
2000	28	71	20	6	0.71 : 1	0.62 : 1
2001	42	74	29	21	0.69 : 1	
$\bar{x}$ or total	88	74	68	19	0.77 : 1	0.72 : 1

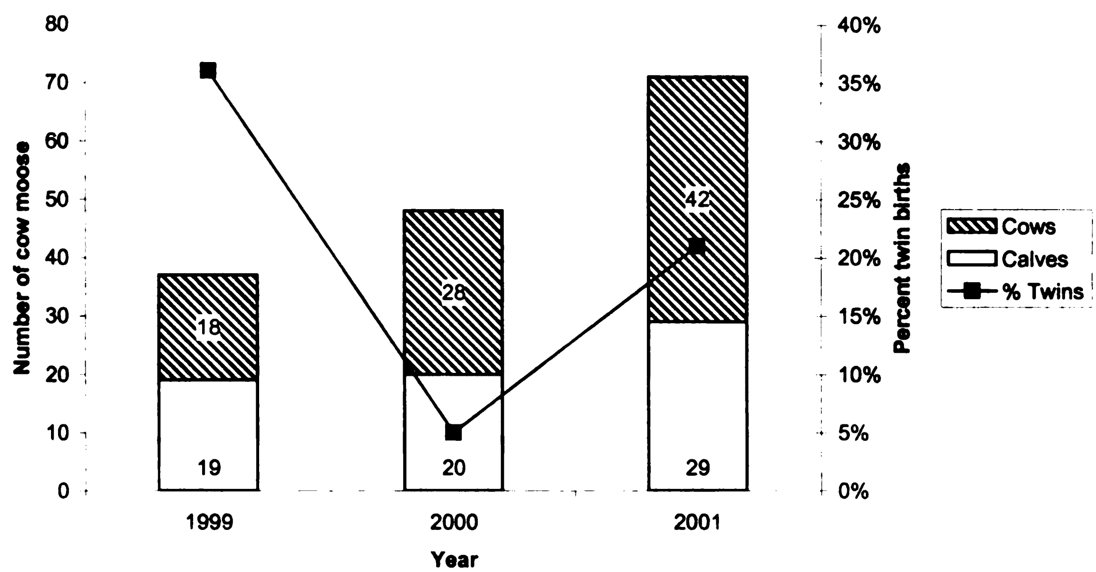

Figure 19. Numbers of radio-tagged cow moose, their spring calf production, and observed spring twinning rates in the western Upper Peninsula of Michigan, 1999-2001.

decreased from 1.06 to 0.76 in 1999-2000 (-28%) and from 0.71 to 0.62 (-13%) in 2000-2001. Post-calving calf:cow ratios for 2001-2002 were unavailable because the study ended on 30 June 2001.

Population size estimation and projection

It needs to be emphasized that, although POP-II is generic (i.e., it can be used to estimate the population size of any species in any geographic location), the survival and reproductive values used in the model are unique to the population of interest. Therefore, the moose population size estimates produced by POP-II are unique to the western Upper Peninsula and immediate region only. Population size estimates (or simulations) were made for 15 years (1987-2001) starting with a population of 103 moose (the estimated 1987 post-partum population), consisting of 65 adults, 9 yearlings, and 29 calves.

Using the MDNR (1985-1996) values of adult $\hat{S}$=0.87, calf $\hat{S}$=0.83 and calf:cow=0.84 (Table 15) resulted in an estimated population of 812 moose by 2001 with a finite rate of increase (λ) of 1.158. In comparison, the population size estimate for 2001 using the MSU (1999-2001) values of adult $\hat{S}$=0.88, calf $\hat{S}$=0.71 and calf:cow=0.81 was 44% smaller (455 moose, λ=1.112). When 6% annual yearling dispersal was added, the result was a 13% smaller population size (395 moose, λ=1.101) than without dispersal (Figure 20).

I examined the influence of calf survival by comparing the population size estimates obtained using the MSU (1999-2001) calf $\hat{S}$=0.71 to that using the MDNR (1985-1996) calf $\hat{S}$=0.83. As a control, adult $\hat{S}$ and the calf:cow ratio were averaged over both studies (adult $\hat{S}$=0.88, calf:cow=0.84). The higher calf $\hat{S}$ resulted in a 49% larger population size by 2001 (739 moose, λ=1.151) than the result using the lower calf $\hat{S}$ (496 moose, λ=1.090) (Figure 21).

The influence of yearling dispersal ($\hat{D}$) was more closely examined by comparing population size estimates obtained if no annual yearling dispersal occurred and if annual yearling $\hat{D}$ were 0.06 or 0.12. The above control parameters (adult $\hat{S}$=0.88, calf:cow=0.84) and a mean calf $\hat{S}$= 0.77 were used. Without dispersal the population size estimate was 608 moose (λ=1.135) by 2001. In comparison, the estimate of the 2001 population size was 14% smaller (523 moose, λ=1.123) when annual yearling $\hat{D}$=0.06 and 26% smaller (448 moose, λ=1.110) when annual yearling $\hat{D}$=0.12 (Figure 22).

Table 15. Reproductive parameters of radio-tagged cow moose and survival of their offspring during 1985-1990, 1995-1996 in the western Upper Peninsula of Michigan (Source: MDNR files, Marquette, Michigan).

Year[ab]	No. cows	No. calves	Calves per 100 cows	Calf $\hat{S}$[c]
1985	17	21	123	0.76
1986	14	10	71	0.90
1987	27	30	111	0.80
1988	23	27	117	0.81
1989	16	17	106	0.71
1990	16	12	75	[d]ND
1995	10	7	70	0.86
1996	10	5	50	1.00
All years combined	133	129	91	0.83

[a] Spring calving checks not conducted in 1991-93.
[b] Small sample of cows precluded use of data in 1994, 1997-1998
[c] Simplistic estimator.
[d] ND - No data available.

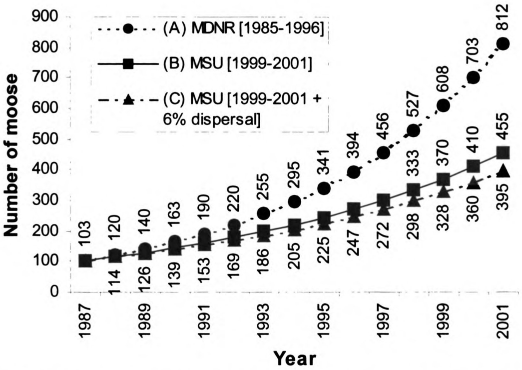

Figure 20. POP-II moose population size estimates in the western Upper Peninsula of Michigan, 1987-2001. Results reflect the use of: **(A)** adult $\hat{S}$=0.87, calf $\hat{S}$=0.83, calf:cow=0.84, **(B)** adult $\hat{S}$=0.88, calf $\hat{S}$=0.71, calf:cow=0.81 and **(C)** adult $\hat{S}$=0.88, calf $\hat{S}$=0.71, calf:cow=0.81 and yearling $\hat{D}$=0.06.

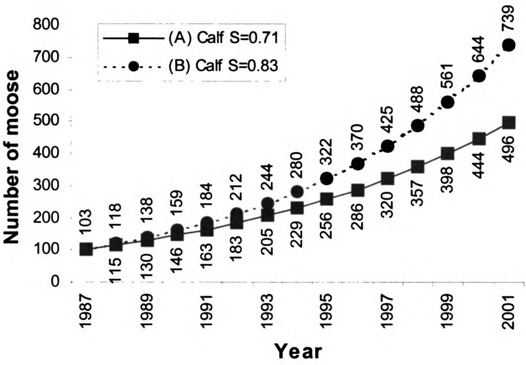

Figure 21. POP-II moose population size estimates in the western Upper Peninsula of Michigan, 1987-2001. Results reflect the use of adult $\hat{S}$=0.88, calf:cow=0.84 and **(A)** calf $\hat{S}$=0.71 and **(B)** calf $\hat{S}$=0.83.

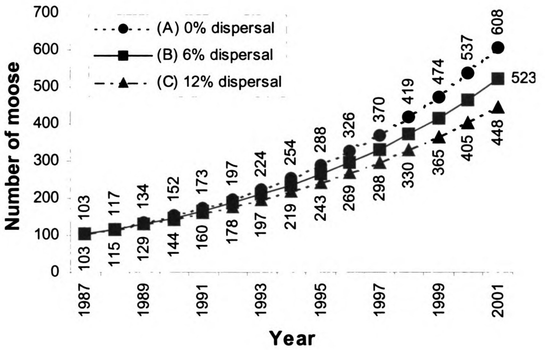

Figure 22. POP-II moose population size estimates in the western Upper Peninsula of Michigan, 1987-2001. Results reflect the use of adult $\hat{S}$=0.88, calf $\hat{S}$=0.77, calf:cow=0.84 and an yearling $\hat{D}$ of **(A)** 0.00, **(B)** 0.06 and **(C)** 0.12.

DISCUSSION

Survival and mortality

Survival rates of moose in the western Upper Peninsula (Table 2, Table 3) were comparable to other non-hunted moose populations where predation by wolves and bears is minimal. In north-central Alberta Canada, Mytton and Keith (1981) reported mean annual survival rates of 0.86 for adults and 0.83 for yearlings. In addition, the mean survival rate of calves $\leq$ 7-months of age was 0.67, which they believed to be a good estimate of first-year survival. In a newly established moose population in southwest Colorado, Olterman and Kenvin (1998) reported only slightly higher mean annual bull survival (0.94, 1%>) and a similarly lower mean annual cow survival (0.83, 2%<) than were found in this study (bull=0.93, cow=0.85). Also, mean annual adult survival in this study ($\bar{x}$=0.877, range=0.873-0.880) was nearly identical to that in Michigan from 1985-1989 ($\bar{x}$=0.871, range=0.818-0.956).

In two separate moose populations (Agassiz National Wildlife Refuge [ANWR] and Beltrami Island State Forest [BISF]) Cox et al. (1997) estimated annual cow survival rates of 0.67 and 0.72, rates that were 22% and 16% lower, respectively, than annual cow survival (0.86) in the western Upper Peninsula of Michigan for 1999-2001. Also, average 1999-2001 winter and summer survival rates of adult moose in the western Upper Peninsula of Michigan (summer=0.95, winter=0.92) were similar to those reported by Cox et al. (1997) at ANWR (summer=0.91, winter=0.89).

Cox et al. (1997) reported 0-6 month calf survival at ANWR of 0.87, which was 3% higher than in the western Upper Peninsula (0.84). However, first-year survival of calves (0.56) and annual survival of yearlings (0.41) at ANWR were 21% and 50% lower than first-year calf survival (0.71) and annual yearling survival (0.82) in this study. In every year except 1985 and 1989, estimates of first-year calf survival in the western Upper Peninsula of Michigan for 1985-1996 (Table 15) were greater than first-year calf survival rates found in the current study (Table 3). This is likely the result of the small sample of calves that were monitored in 1986 (n=10), 1995 (n=7), and 1996 (n=5) and the use of the simplistic survival estimator.

Where predation is a major source of early calf mortality, survival rates of calves are much lower than reported here. For example, in interior south-central Alaska during 1976-1986, Ballard et al. (1991) found that 61% of calves died within the first 5-months of life and that brown bear (*Ursus arctos*) predation accounted for 73% of all calf deaths. The survival of calves ≤ 5-months of age was estimated at 0.39. Also, on the Copper River delta in coastal south-central Alaska, MacCracken et al. (1997) reported calf survival rates of only 0.03 in 1987, 0.24 in 1988, and 0.05 in 1989 and that 94% of calves had died by 30 June each year. This low calf survival was associated with inclement spring weather and predation by brown bears. Predation on neonates may have been higher in this study than was detected, primarily because only un-tagged calves were determined to have died in their first year of life, and their bodies could not be recovered. Nevertheless, compared to the above studies and others in Canada and Alaska (Franzmann, et al. 1980, Ballard et al. 1981, Larsen et al. 1989, Gasaway et al. 1992) predation of neonates in the Upper Peninsula of Michigan by wolves and bears is minimal.

Previous to the current study, 23% (13 of 57) of radio-tagged moose that died were diagnosed with cerebrospinal nematodiasis (i.e., adult *P. tenuis* nematodes were found on the meninges or brain); of these 13 moose, 54% (7) also suffered from malnutrition. During 1999-2001 only 17% (3 of 17) of dead moose were diagnosed with cerebrospinal nematodiasis and of these 3, only 1 was malnourished. Whether malnourished moose are more susceptible to infection by meningeal worms or infection prevents moose from getting adequate nutrition is not known. Currently it does not appear that brain worm is a major contributing cause of moose deaths in the western Upper Peninsula of Michigan. However, if the region experiences a period of mild winter weather and the white-tailed deer density increases, we may see more moose dying from brain worm related problems. In areas managed primarily for moose, Karns (1967) has suggested that white-tailed deer densities be maintained at $\leq$4.6 deer/km^2. The most recent estimate of white-tailed deer density in the western Upper Peninsula of Michigan was 4 to 11 deer/km^2 (Hill 2001). However, the transmission of *P. tenuis* may be more complex, and its long-term effects on moose health less severe than previously suspected (see Lankester and Samuel 1998).

Additionally, prior to the current study 12% (n=7) of radio-tagged moose that died were found to have liver flukes or liver damage evident of them (fibrous scar tissue and/or thick-walled capsules). In this study 44% (n=8) of radio-tagged moose that died were infested with liver flukes. However, alone, the parasite has not been clearly shown to be harmful to moose (Lankester and Samuel 1998). A heavy infestation of liver flukes accompanied by some other ailment, such as malnutrition may contribute to death. All dead radio-tagged moose that had liver flukes (Table 4) were also suffering from other ailments.

Movements

Twenty to 40% of moose in the western Upper Peninsula of Michigan annually migrated between spatially separate winter and summer home ranges (Table 6). Addison et al. (1980), and Phillips et al. (1973) reported similar proportions of migratory moose in northwest Ontario (37%) and northwest Minnesota (20%), respectively.

Migration distances are mainly a function of habitat dispersion or terrain, and therefore, vary both within and among populations (Addison et al. 1980). Generally, moose that inhabit more level terrain migrate shorter distances between seasonal ranges than do those in mountainous regions. Distances between summer and winter ranges in this study (2-26 km) were similar to those reported by Mytton and Keith (1981) in Alberta (bulls, 13 km; cows, 7 km), MacCracken et al. (1997) in coastal south-central Alaska (maximum distances: bulls, 15 km; cows, 25 km), Addison et al. (1980) in northwest Ontario (2-13 km), and Phillips et al. (1973) in northwestern Minnesota (14-34 km). In contrast, the average migration distance between seasonal ranges in interior south-central Alaska was 48 km (range=10-68 km) (Ballard et al. 1991) and southeast of the Brooks Range in Alaska and Canada, 123 km (range=18-196 km) (Mauer 1998).

Moose migrate to summer ranges to optimize nutrient intake, however in the winter these areas may not provide adequate forage or cover (Hundertmark 1998). In mountainous terrain, moose generally migrate from lower elevation winter ranges to higher elevation summer ranges (Ballard et al. 1991). Although the opposite elevation movement pattern has been observed (Gasaway et al. 1983, Mauer 1998). In the relatively non-mountainous Great Lakes region of the coniferous-deciduous ecotone, moose often migrate in the spring to poorly drained areas dominated by black spruce (*Picea mariana*) and interspersed with bogs and lakes (Van Ballenberghe and Peek 1971, Phillips et al. 1973, Peek et al. 1976). In addition to the palatable, high quality aquatic vegetation (e.g., *Equisetum* spp, *Nuphur* spp.) that is available and consumed by moose in these lowland areas, they may also provide escape from insects and safe calving sites for cows.

Migration to winter ranges occurs in response to seasonal changes in forage plant species (i.e., leaf abscission and plant dormancy) and in the availability of these plants because of snow accumulation. Many authors, for example Addison et al. (1980), MacCraken et al. (1997), and Sweanor et al. (1992) found that late-autumn and winter migrations began when snow depths approached 50-60 cm. In the early part of winter in eastern North America, moose are often found in areas with a comparatively open canopy and well-developed undergrowth of coniferous and deciduous regeneration. Later, when snow depths begin to cover available forage, moose move to dense spruce-fir forests where snow depths are less. Thereafter, if snow conditions improve, moose may move into open woodlands to feed and return to dense spruce-fir forests to bed-down (Telfer 1970, Peek et al. 1976, McNicol et al. 1980). In Michigan in early winter, Minzey and Robinson (1991) found moose in relatively open (<50% canopy closure) hardwood stands dominated by sugar maple. However, later in winter, moose sought out areas with a dense overstory (50-70% canopy closure) of balsam fir and eastern hemlock. In the present study, the proportion of seasonally migratory moose and their movement patterns were generally typical of those reported for moose in the Great Lakes region.

Because of the numerous methods used to estimate home range size, and the different algorithms and parameter values that software programs incorporate to apply these methods, it is often difficult to make comparisons to other studies (Lawson and Rogers 1997). The MCP method is the oldest (Mohr 1947) and most frequently used estimator of home range size (Harris 1990). However, the technique is severely affected by sample size (White and Garrot 1990, Boulanger and White 1990) and the distribution of outlying points (Kenward 2001). Ballard et al. (1991) found that ≥ 40 relocations were needed to adequately define 75% of total home range sizes of moose using the MCP method. Probabilistic methods, such as the FK are better estimators than the MCP approach because (1) they are not as severely affected by sample size, (2) home range boundaries are based on the complete distribution of relocation points, and (3) they can better handle outliers (Kernohan et al. 2001). Kernel methods were introduced as home range estimators by Worton (1989), but have only recently become popular as more software has become available (Seaman et al. 1998). Only 1 study in the literature was found that used the fixed kernel method to estimate moose home ranges and only winter ranges were reported. Therefore, unless otherwise specifically stated, all of the studies referred to below used the MCP home range estimator. How authors define their seasonal time periods further complicates comparisons of seasonal ranges between studies.

Estimates of mean 95%-FK summer home ranges in this study (4-115 km^2, Table 6) were smaller than those found by Ballard et al. (1991) in interior south-central Alaska (23-456 km^2), by MacCracken et al. (1997) in coastal south-central Alaska (21-162 km^2), and by Stenhouse et al. (1995) in the Northwest Territories (68± 35 km^2). Smaller summer home range estimates were found in northwest Minnesota (1.5-24 km, Phillips 1973, home range fill method), Central Alberta (1-34 km^2, Mytton and Keith 1981), and northern New York (36.3 km^2, bulls only, Garner and Porter 1990). Similarly sized estimates of summer home ranges were noted by Hauge and Keith (1981) in northeast Alberta (18-97 km^2) and Addison et al. (1980) in northwestern Ontario (6-90 km^2).

Average 95%-FK estimates of the size of winter home ranges in the western Upper Peninsula of Michigan (1-64 km^2, Table 6) were smaller than those found in interior south-central Alaska (15-375 km^2, Ballard et al. 1991), coastal south-central Alaska (19-146 km^2, MacCracken et al. 1997), and the Northwest Territories (57± 58 km^2, Stenhouse et al.1995). Winter home range estimates were larger than those found by Phillips (1973) in northwest Minnesota (0.5-5.0 km^2, home range fill method), Addison et al. (1980) in northwest Ontario

(2-12 km^2), and Garner and Porter (1990) in northern New York (7.5 km^2, bulls only). Estimates of winter home range sizes similar to the findings of this study were noted by Lawson and Rogers (1997) in northwest Ontarion (33 km^2, Fixed Kernel estimator), Mytton and Keith (1981) in central Alberta (2-54 km^2) and Hauge and Keith (1981) in northeast Alberta (3-111 km^2).

The winter movements and size of winter home ranges of moose are likely influenced by snow depth. During extended periods of deep snow (>70 cm), moose often restrict their movements to relatively small areas where snow is not as deep, thus influencing the overall size of their winter home range. For example, in northern Maine, winter home ranges (median=7.1 km^2) were nearly 4.5 times larger during a winter when snow depths were low compared to when they were >70 cm (median=1.6 km^2) (Thompson 1987). In this study no difference (P=0.5372) was detected between the movements of cows in winter compared to other times of the year (Table 5). Because the influence of snow depth on winter home range size was not closely examined during this study no strong conclusions can be made. However, 2 adult cows, for which consecutive winter home range estimates were obtained, occupied different sized areas from one winter to the next. But the trend was not the same for each animal. Moose, No. 76, had a larger winter home range in 1999-00 (16 km^2) than in 2000-01 (5 km^2), whereas moose No. 121, had a smaller winter home range in 1999-00 (25 km^2) than in 2000-01 (42 km^2). Although we often found snow depths >70cm during the present study, mean daily snow depth never exceeded 60 cm and no rapid movements of moose were noticed following early winter snowstorms.

There is no consistent trend that moose have larger (or smaller) home ranges in the winter than in the summer (Hundertmark 1998). In this study, median home ranges of resident and migratory adult moose combined were greater in the summer than in the winter. Addison et al. (1980) and Garner and Porter (1990) also found that moose had larger summer than winter home ranges. In contrast, Doerr (1983) found that moose had larger winter home ranges, whereas Ballard et al. (1991), Hauge and Keith (1981) and Stenhouse et al. (1995) found no difference between the size of seasonal home ranges. Males typically have larger home ranges than females (Hundertmark 1998, Ballard et al. 1991) due to their greater movements in the fall during the rut (Hauge and Keith 1981). Although no studies reported the opposite, Phillips et al. (1973), Hauge and Keith (1981), MacCracken et al. (1997), and this study found no difference between the size of male and female home ranges. Ultimately, season, habitat quality, interspersion of habitat components, terrain, population density, age, sex and weather influence the size of areas occupied by moose.

All offspring eventually separate from their dams, either voluntarily or by being driven off. Separation generally occurs as parturition approaches, but a full and permanent parting may not occur until sometime during the offspring's second year of life (Hundertmark 1998). In this study all radio-tagged offspring (n=26) had broken completely from their cows at around 1-year of age. Fourteen radio-tagged offspring were closely followed for up to 1-year following separation to analyze their movements. Six offspring occupied areas that spatially overlapped their cow's home range and were often found within close proximity to her for several months after separation. Three offspring completely abandoned the areas occupied by their cow shortly following separation, and 5 (19% of all offspring) dispersed out of the core study area. Ballard et al. (1991) reported that 9 of 15 offspring partially (n=4) or fully dispersed (n=5) from their parental home range, and that more male than female offspring dispersed. In most mammals, juvenile males are more likely to disperse than other individuals, although other age and sex classes are represented (Greenwood 1980). No sex-biased dispersal was noticed in this study, but all moose that dispersed except 1 were yearlings. There are a limited number of reports in the literature regarding moose dispersal and nowhere, were actual dispersal rates stated. Lynch (1976) noted that 50% of subadults (<2-years of age) and 17% of adult moose dispersed off his study area in central Alberta. However, because he considered moose for which radio contact had been lost to have dispersed, these values may be high. In north-central Alberta, Mytton and Keith (1981) documented long distance dispersal movements of at least 50 km for 3 young moose, and 1 yearling bull moved 250 km off the study area over a 2-year period. In the western Upper Peninsula of Michigan, Aho et al. (1995) reported that a yearling female, over a 9-month (March 1989-December 1990) and a yearling male, over a 7-month period (March 1989-December 1990) emigrated at least 160 km to Wisconsin (Figure 23). These moose and their movements are notable because (1) they were born 5-years apart to the same cow, and (2) their dispersal routes, and final destination in Wisconsin were very similar to each other, and to 2 moose in the current study (Figure 12, Figure 16).

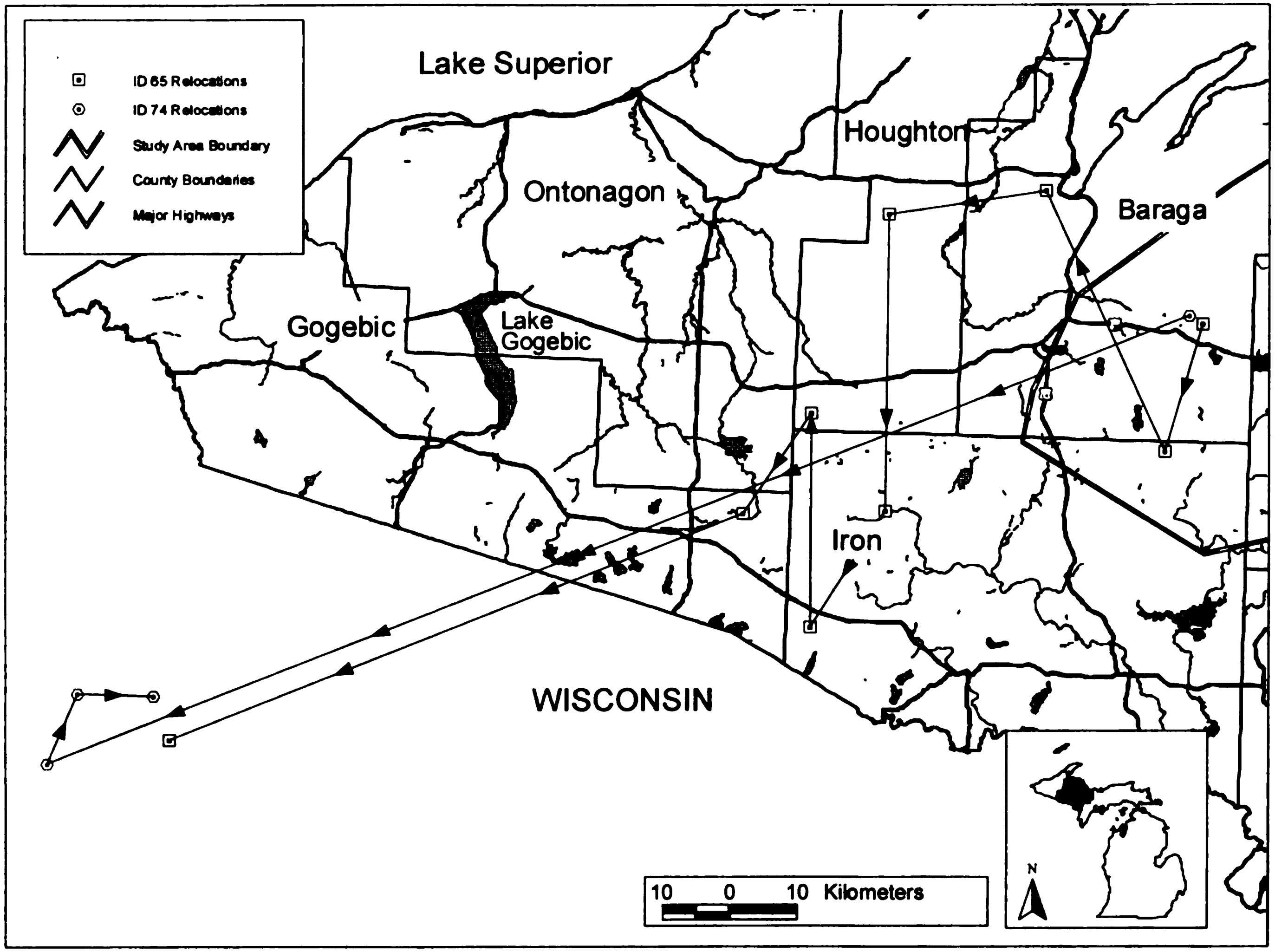

Figure 23. Estimated relocation points and movements of radio-tagged yearling female moose (No. 65) during March 1989-December 1990, and yearling male moose (No. 74) during March-October 1994 in the western Upper Peninsula of Michigan.

Although the exact mechanisms prompting dispersal are multifaceted and complex, population density in relation to habitat productivity and social stress appear to be two important factors (Ballard et al. 1991).

Reproduction and productivity

Moose pregnancy rates in the western Upper Peninsula of Michigan ($\bar{x}$=74%) were lower than those in the Northwest Territories (96%, Stenhouse et al. 1995), but higher than those in 2 moose populations in northwest Minnesota (ANWR=37.5%, BISF=51%, Cox et al. 1997). In his review of 12 studies that reported information on moose reproduction, Boer (1992) found relatively constant adult pregnancy rates across North America ($\bar{x}$=84%, range=77-97%). Although pregnancy rates in this study were 7 to 15% lower than the North American average, they were fairly consistent from year to year (Table 14). The rates reported here were most similar to the 79% found by Boer (1987) and the 76% of Edwards and Ritcey (1958).

Yearling pregnancy rates, unlike adult pregnancy rates are less stable. Among different moose populations, Boer (1992) found that pregnancy rates of yearlings averaged 42% and ranged from 0 to 93% (CV=69%). Furthermore, within the same moose population, Blood (1974) reported that 15 to 93% ($\bar{x}$=29%, CV=89%) of yearlings were pregnant. Although the number of potentially reproducing yearling females (n=10) in this study was small, it appears that yearling pregnancy rates in the western Upper Peninsula (10-30%) are very low compared to other moose populations in North America.

Twinning rates also vary considerably among moose populations in North America (Boer 1992, Schwartz 1997). Values from as low as 1% in southern Newfoundland (Albright and Keith 1987) to as high as 88% in north-central Alberta (Mytton and Keith 1981) have been recorded. Lower rates (<5%) are indicative of populations above carrying capacity, whereas moderate (5-25%) and higher (25-90%) rates are associated with populations near and below carrying capacity, respectively (Gasaway et al. 1992, Schwartz 1997). Although the average observed twinning rate reported in this study (19%) fell in the range of rates for populations near carrying capacity, among years, each rate fell into a different carrying capacity category (Table 14, Figure 19). An evaluation of available habitat in the western Upper Peninsula indicated that the moose population is apparently below carrying capacity (Patterson et al. 1995). In south-central Alaska, Ballard et al. (1991) reported twinning rates which ranged from 17 to 63% that varied by year, area, and possibly collection method, and Blood (1974) reported that they ranged from 4 to 48% at Elk Island National Park, Edmonton, Alberta. For the period 1985-1995, MDNR wildlife biologists reported an average twinning rate of 36% that was also highly variable (range=24-69%, Aho et al. 1995).

Population size estimation and projection

Population models are useful tools that are often used to assist in formulating management strategies and making decisions. The type and complexity of the model needed is driven by the objectives of the study. For the purposes of this study (i.e., comparisons between estimates using different input variables), a deterministic model, such as POP-II is adequate. Because the results of deterministic models are based on fixed input variables, it is critical that the values of these variables are accurately estimated. This requires that an adequate and representative sample of animals is radio-tagged. For survival analysis, Winterstein et al. (2001) suggests that >25 animals, per treatment (e.g., sex, age class) are radio-tagged. From 1985 to 1990 the number of radio-tagged adult moose varied from 22 to 50, which permitted fairly accurate estimates of adult moose survival. However, after 1990, despite the MDNRs attempts to maintain an adequate sample size - through periodic darting and radio-collaring of moose, and the capture and radio-collaring of 26 moose from a helicopter in 1995 - the number of radio-tagged moose at any one point in time was probably insufficient to provide accurate results. Additionally, the Simplistic estimator used by the MDNR to estimate survival, does not permit staggered entry of newly radio-tagged individuals and is biased if animals are censored (see Winterstein et al. 2001). Estimates of natality (calves per cow), prior to 1991, were also fairly accurate, but became less accurate thereafter because (1) spring calf checks were suspended during 1991-1993, and (2) the number of radio-tagged cows in any one year during 1994-1998 was <10.

Inconsistencies in data collection, periodically inadequate sample sizes and the use of a biased survival estimator call into question the accuracy of the 1985-1996 values of moose survival and reproduction and the population size estimates derived from these values. Because a more robust survival estimator was used and the sample size per treatment was larger, more accurate moose survival rates were obtained during 1999-2001. Additionally, more intensive monitoring of radio-tagged cows and their offspring resulted in better estimates of reproduction and calf survival.

Using the survival and reproductive rates obtained during 1999-2001 POP-II produced 15-year moose population estimates of 395 moose (λ =1.101) with dispersal and 455 moose (λ =1.112) without dispersal (Figure 20). In addition, preliminary Mark-Resight population estimates from the 2002 winter aerial survey extrapolated to include all high-density stratum were 448 moose (0.28 moose/km^2) from a fixed-wing aircraft and 467 moose (0.29 moose/km^2) from a helicopter. Based on the above estimates of moose population size, information found in MDNR documents and published reports, conversations with MDNR wildlife biologists and my involvement in the current study, an estimated population of 400-500 moose in the western Upper Peninsula of Michigan is reasonable.

LIMITING FACTORS

One of the objectives of this study was to identify the factors that could be limiting the growth of the moose population in the western Upper Peninsula of Michigan. As defined by Gasaway et al. (1992), "limiting factors retard the rate of increase in population size or density through density-dependent and/or density-independent processes". Evidence indicates that the moose population in the western Upper Peninsula is likely below carrying capacity and density-dependent processes, such as competition for food, are not operating. Predation, disease, snow accumulation >90 cm. and nutrition have been identified as the primary factors that have the potential to limit moose population growth. In the following paragraphs the impact of these factors on moose population growth in the study area will be assessed.

Predation by wolves and bears (black and/or brown) combined, has been shown to keep moose at low densities for extended periods of time (Gassaway et al. 1992). Although the Upper Peninsula of Michigan supports a healthy black bear population (n>12,000) and an increasing wolf population (n=200-250), there seems to be little predation on moose. Only 1 confirmed case of a wolf-killed moose was made during the current study, and of the 43 moose deaths reported from 1985-1994, none was attributed to wolf or black bear predation (Aho et al. 1995).

No evidence was found to indicate that disease or parasites is limiting the growth of the moose population in the western Upper Peninsula. Moose are susceptible to many diseases, viruses, and parasites, but the population regulating effects of these are largely unknown or of little consequence. Necropsies determined that only 3 moose likely died of brain worm and that 8 were parasitized with liver flukes. However, in almost every case these animals had additional maladies that likely contributed to their deaths (Table 4).

There was no evidence that severe winter weather or deep snow had a large impact on moose survival and reproduction. Average snow depths were <70 cm, the level above which adult moose may have difficulty travelling and reaching browse, and large losses of calves has been recorded in interior Alaska (Gasaway et al. 1983). Although snow depths >70 cm were often found where fecal samples were collected, movements of moose did not appear to be restricted. Furthermore, first-year calf survival was lower in 1999-00 (0.63) than in 2000-01 (0.78) when snow depths were greater.

Nutritional stress has the potential to limit population growth irrespective of the density of the population. Although, at high density, increased competition for food resources make certain classes of the population (e.g., calves, pregnant cows, rutting bulls) more vulnerable to malnutrition. Possible signs of acute nutritional stress include, low adult survival and retarded body growth, reduced recruitment and low calf survivorship, poor physical condition and starvation prior to old age, and poor reproductive output (Messier and Crête 1984, Gasaway et al. 1992). The quality, quantity, and availability of forage ultimately determine an animal's nutritional status. Therefore, the marginal habitats often found at the periphery of an animal's range likely effect its nutritional condition. No studies have yet, however looked at the consequences of marginal habitat on moose nutrition and its effect on survival and fecundity.

The manifestations of nutritional stress were not reflected in moose survival, recruitment, physical condition, body growth or longevity. Annual adult survival was relatively high (>85%) during both years. Calf survival and recruitment were comparable to other moose populations where predation is low. In addition, analysis of blood samples collected during capture, and physical examination score ($\overline{x}$=8.5$\pm$0.15, range=2-10) indicate that moose are in adequate physical condition for early winter. Also, only 3 of 12 adult moose that died, for which marrow fat analysis was done, had femur marrow fat levels <20% indicating severe malnutrition (Peterson et al. 1984).

On the other hand, marginal nutrition, the result of less than optimal forage, could be the reason for the below average pregnancy rates and low twinning observed in this study. Crête and Courtois (1997) claimed that the low fecundity of moose in east central Québec at the northern extent of moose range, was the result of suboptimal production of summer and winter forage. They attributed this low productivity to the mature age of the forest stands and absence of recent disturbances, and the unsuitability of a large portion of the plant communities on the study area. Franzmann and Schwartz (1995) demonstrated that twinning rates might also be a good indicator of nutritional status and indirectly of habitat quality. On the Kenai Peninsula of Alaska, they found that 70% of cow moose living on high quality habitat, gave birth to twins, whereas on poor quality habitat only 20% of cows produced twins. Furthermore, Boer (1992) found a direct relationship between adult twinning rates and yearling pregnancy rates. Yearlings that are well nourished grow faster, mature earlier and frequently breed and give birth to a single calf (Schwartz and Hundertmark 1993). The relationship between forage, nutrition, and reproduction is intuitive, but no study has yet related forage quality, quantity, and availability to moose fecundity (Crête and Courtois 1997).

A coarse evaluation of habitat suitability in Baraga County using historic information and remotely sensed forest cover data indicated that the available habitat in the county could support between 1094 and 1845 moose depending on which data-set was used (Patterson et al. 1995). Also, the relatively young age of many forest-stands and the intensity of logging and natural disturbance in the western Upper Peninsula would suggest that forage productivity and quality is good. However, habitat suitability has to be verified on the ground and a more quantitative analysis of forage productivity should be conducted before eliminating these factors as sources of nutritional deficiencies.

Moose inhabiting the Upper Peninsula of Michigan are at the southern limit of moose range in the non-mountainous regions of North America. Given this, the habitat and climatic conditions that have prevented further range expansion of moose in the region may also be limiting their population growth in the western Upper Peninsula of Michigan.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

The 1985 and 1987 translocations of moose from Ontario Canada to the western Upper Peninsula of Michigan generated great excitement and high expectations. Although some of this enthusiasm has waned, there is still great interest and some concern, both among the citizenry and wildlife biologists of Michigan regarding the slower than expected growth of the moose population. However, this concern may be unwarranted. The original population goal of 1000 moose in the western Upper Peninsula by the year 2000 was overly optimistic. It is important to inform personnel within the MDNR and the general public that from most indications the moose herd is currently faring well. It should also be conveyed that the number of moose in the Upper Peninsula of Michigan might never reach 1000.

Brain worm is another issue that needs to be clarified. Popular articles and MDNR reports inadvertently over emphasized the negative effect of *P. tenuis* on the moose population. Recent experiments have shown that moose infected with *P. tenuis* do not always exhibit clinical signs of the disease, nor is infection always fatal. It appears that the consequences of infection are both dose and age dependent (Lankester and Samuel 1998). Also, because moose have historically coexisted and continue to coexist with white-tailed deer infected with *P. tenuis*, the extent to which the disease effects moose populations needs further investigation.

The current study of the population dynamics of moose in the western Upper Peninsula of Michigan is being conducted, in part, to determine why 2 independent methods, a deterministic population model and aerial surveys produced drastically different population size estimates. The study is divided into 2, 3-year phases. The primary focus of Phase-I, my portion of the study, was to determine the current rates of moose survival, reproduction, and dispersal. Phase-II, which began in the winter of 2001, will concentrate on evaluating the aerial survey methodology and sightability model as well as estimating the "true" size of the moose population. Although the focus has changed, intensive monitoring of moose survival, reproduction, and movements will continue for at least the next 3 years. Weekly monitoring of radio-collared moose for timely recovery of mortalities is taking place. Also, collection of fecal samples for pregnancy determinations and evaluation of stress levels is ongoing and natality checks will be done in the spring each year. Several more seasons of collecting this data will hopefully provide a more complete understanding of moose population dynamics.

As with most wildlife research, the findings from this study generated further questions, pointing to the need for more research, much of which is currently being conducted. The study did reveal the answer as to why the moose population in the western Upper Peninsula has not increased as quickly as predicted. Low reproduction, exhibited in (1) below average adult reproductive rates, (2) low adult twinning rates, and (3) extremely low yearling reproductive rates is the reason for the slow population growth. The more important question and more difficult one to answer is, Why is moose reproduction low? And, should we be concerned? Or, is low reproduction endemic to this moose population at the southern edge of its range?

Because nutrition plays such an important role in reproduction, an analysis of the nutritional quality and productivity of the available forage in the western Upper Peninsula is warranted. This information would indicate how well (or poorly) the habitat in the western Upper Peninsula is meeting the year round nutritional and energetic requirements of moose. As a preliminary step, I began collecting samples of terrestrial and aquatic plants both incidentally and those browsed by moose. Plants were analyzed for selenium (Se), a trace element that has been linked to white muscle disease, low reproduction and reduced fertility primarily in livestock. We were specifically interested in Se because the mean whole blood Se levels of moose radio-tagged in 1999 was only 0.036-ppm, a level considered deficient by livestock standards (<0.04-ppm, Oliver 1990). Preliminary analysis found no detectable levels of Se in the plants collected. Because forage and grain plants grown in Michigan for livestock consumption are deficient in Se (Kubota and Allaway 1972) these results were not unexpected. However, the Se requirements of free-ranging moose are not known and the relationship between moose health and Se is not as yet completely understood.

Also, although moose appear to be in adequate health condition in the winter, their summer health condition is unknown. Extended periods of high summer temperatures may cause heat stress and interfere with feeding, which could ultimately effect moose body growth, fat storage, and reproduction.

Assays of fecal glucocorticoid steroids have been used to study physiological stress in elk (*Cervus elephus*) in North Dakota (Millspaugh et al. 2001). Moose fecal samples, collected primarily in the winter, were analyzed by Dr. Millspaugh's lab at the University of Missouri this past year for glucocorticoid levels. However, base-line glucocorticoid levels for moose need to be established before comparisons among individuals can be made. Nevertheless, the collection of fecal samples in the summer (in addition to those collected in the winter) and analysis of these samples for glucocorticoid levels would permit comparisons between summer and winter stress levels of moose.

Finally, a stochastic model that allows survival, reproduction, and dispersal rates to vary randomly and uses the statistical distribution of these values rather than their means would probably produce more accurate estimates of the moose population in the western Upper Peninsula of Michigan. In addition, climatic conditions such as snow depth and a summer severity index could be incorporated into such a model.

APPENDIX

Appendix Table 1[a,b]. Records of moose sightings or evidence of moose by county in Michigan's Upper Peninsula, 1954-1966.

	1954-1960				1961-1966			
County	Bulls	Cows	Calves	Unknown[c]	Bulls	Cows	Calves	Unknown[c]
Alger	5	5		10	1	1		5
Baraga								
Chippewa	12	13	6	7	2	2		5
Delta	1				2	4	1	5
Dickinson								
Gogebic								
Houghton								
Iron				3				
Keweenaw								
Luce	1			4				12
Mackinac				1		1		
Marquette	1			1		2	1	6
Ontonagon								
Schoolcraft	1			4	3			5
Total	21	18	6	30	8	10	2	38

[a] Adapted from MDNR Wildlife Division Report No. 2973 by Verme 1984.
[b] Based on records on file at the Cusino Research Station, Shingleton, Michigan, which are possibly incomplete.
[c] Includes moose of unknown sex and age, and evidence of moose (e.g., tracks, pellets).

Appendix Table 2[a,b]. Records of moose sightings or evidence of moose by county in Michigan's Upper Peninsula, 1967-1983.

	1967-1972				1973-1983			
County	Bulls	Cows	Calves	Unknown[c]	Bulls	Cows	Calves	Unknown[c]
Alger				3	2			1
Baraga	9	4		3	1	2	1	1
Chippewa	10	13	4	19	7	12	2	31
Delta	1			3	3			
Dickinson					1		1	
Gogebic		1			1			
Houghton	3			1				
Iron					2	1		
Keweenaw								
Luce	3			11	3		1	17
Mackinac	1	4	2	8	3	1		29
Marquette	1	1		2	7	1		
Ontonagon	3	1	1		2			3
Schoolcraft				2	6	2		9
Total	31	24	7	52	38	19	5	91

[a] Adapted from MDNR Wildlife Division Report No. 2973 by Verme, 1984.
[b] Based on records on file at the Cusino Research Station, Shingleton, Michigan, which are possibly incomplete.
[c] Includes moose of unknown sex and age, and evidence of moose (e.g., tracks, pellets).

Appendix Table 3. Physical examination scores and description for assessing moose condition during capture and when conducting field necropsies[a].

Score	Description of condition
10	A prime fat moose with thick firm rump by sight. Well fleshed over back and loin. Shoulders round and full.
9	A choice fat moose with evidence by feel of rump fat. Fleshed over back and loin. Shoulders round and full.
8	A good fat moose with slight evidence by feel of rump fat. Bony structures of back and loin not prominent. Shoulders well fleshed.
7	An "average" moose with no evidence of rump fat but well fleshed. Bony structures of back and loin evident by feel. Shoulders with some angularity.
6	A moderately fleshed moose beginning to demonstrate one of the following conditions: (a) definitions of neck and shoulders, (b) upper foreleg musculature distinct from chest, or (c) prominent rib cage.
5	When two of the characteristics in class 6 are evident.
4	When all three of the characteristics in class 6 are evident.
3	When the hide fits loosely about the neck and shoulders.
2	Malnutrition obvious. Outline of the scapula is evident.
1	Point of no return
0	Dead from malnutrition/starvation.

[a] Adapted from Franzmann 1998.

Appendix Table 4. Moose id, sex, age at capture, date captured, type of radio collar, and fate as of 30 June, 2001 of radio-tagged moose studied during 1999-2001 in the western Upper Peninsula of Michigan.

Moose id	Sex	Age at capture[a]	Date captured	Last located	Radio collar type[b]	Fate[c]
28	F	A	1 Feb 1995	7 Jun 2001	VHF	Alive
70	M	A	1 Feb 1995	22 Jun 2001	VHF	Alive
73	F	A	1 Feb 1995	29 Jun 2001	VHF	Alive
74	M	A	1 Feb 1995	18 Aug 2000	VHF	Dead
75	F	A	1 Feb 1995	7 Jun 2001	VHF	Alive
76	F	A	2 Feb 1995	12 Jun 2001	VHF	Alive
77	M	A	1 Feb 1995	27 Jun 2001	VHF	Alive
78	M	A	31 Jan 1995	11 Jun 2001	VHF	Alive
79	M	A	31 Jan 1995	22 Jun 2001	VHF	Alive
80	F	A	1 Jan 1995	30 Oct 1999	VHF	Dead
86	F	A	1 Jan 1995	26 Jun 2000	VHF	Dead
92	M	A	2 Feb 1999	22 Jun 2001	VHF	Alive
101	M	C	30 Jan 1999	2 Feb 1999	VHF	Dropped
102	F	Y	29 Jan 1999	9 Apr 2001	VHF	Dead
103	M	C	30 Jan 1999	29 Jun 2001	VHF	Alive
104	M	C	30 Jan 1999	4 Jun 2001	VHF	Alive
105	F	C	30 Jan 1999	3 Jul 2000	VHF	Dropped
106	M	C	29 Jan 1999	19 Sep 1999	VHF	Dead
107	M	C	30 Jan 1999	16 Nov 2000	VHF	Dead
108	F	Y	31 Jan 1999	11 Jun 2001	VHF	Alive
109	F	C	28 Jan 1999	7 Jun 2001	VHF	Alive
110	F	C	28 Jan 1999	31 Oct 2000	VHF	Dead
111	F	C	29 Jan 1999	16 Jun 2001	VHF	Alive
112	M	C	31 Jan 1999	22 Jun 2001	VHF	Alive
113	M	C	28 Jan 1999	14 Apr 2001	VHF	Dropped
114	M	C	7 Feb 1999	27 Mar 2000	VHF	Dead
115	F	A	7 Feb 1999	17 Dec 2000	VHF	Dead
116	F	A	31 Jan 1999	7 Jun 2001	VHF	Alive
117	F	A	31 Jan 1999	27 Jun 2001	VHF	Alive
118	F	A	30 Jan 1999	11 Jun 2001	VHF	Alive
119	F	A	30 Jan 1999	11 Nov 1999	VHF	Dead
120	F	A	28 Jan 1999	29 Jun 2001	VHF	Alive
121	F	A	2 Feb 1999	29 Jun 2001	VHF	Alive
122	F	A	30 Jan 1999	7 Jan 2000	VHF	Dead
123	F	A	29 Jan 1999	22 Jun 2001	VHF	Alive
124	F	A	7 Feb 1999	22 Jun 2001	VHF	Alive
125	F	A	29 Jan 1999	29 Jun 2001	VHF	Alive
127	M	A	1 Oct 1998	27 Jun 2001	VHF	Alive
130	F	A	19 Jan 2000	29 Jun 2001	VHF	Alive

Appendix Table 4. (Continued).

131	M	2	20 Jan 2000	5 Jun 2001	VHF	Alive
132	F	2	20 Jan 2000	29 Jun 2001	VHF	Alive
133	F	A	20 Jan 2000	25 Apr 2000	GPS	Off line
134	F	2	20 Jan 2000	29 Jun 2001	VHF	Alive
135	M	A	20 Jan 2000	22 Jun 2001	VHF	Alive
136	F	A	21 Jan 2000	21 Apr 2000	GPS	Off line
137	M	A	22 Jan 2000	16 May 2000	GPS	Off line
138	M	2	19 Jan 2000	29 Jun 2001	VHF	Alive
139	F	A	19 Jan 2000	17 Jun 2001	VHF	Alive
140	F	A	19 Jan 2000	7 Jun 2001	VHF	Alive
141	M	2	19 Jan 2000	11 Jun 2001	VHF	Alive
142	M	2	19 Jan 2000	22 Jun 2001	VHF	Alive
143	F	Y	19 Jan 2000	30 Jun 2000	VHF	Dead
144	M	C	19 Jan 2000	3 Apr 2000	VHF	Dead
145	F	A	17 Jan 2000	31 May 2000	VHF	Dead
146	F	A	17 Jan 2000	7 Jun 2001	VHF	Alive
147	F	A	17 Jan 2000	22 Jun 2001	VHF	Alive
148	M	C	17 Jan 2000	29 Jun 2001	VHF	Alive
149	F	C	17 Jan 2000	22 Jun 2001	VHF	Alive
150	F	A	19 Jan 2000	27 Jun 2001	VHF	Alive
151	F	A	15 Jan 2000	16 Jun 2001	VHF	Alive
152	F	A	15 Jan 2000	29 Jun 2001	VHF	Alive
153	M	C	15 Jan 2000	28 Apr 2001	VHF	Dead
154	F	A	15 Jan 2000	22 Jun 2001	VHF	Alive
155	F	A	15 Jan 2000	21 Jun 2001	VHF	Alive
156	F	A	15 Jan 2000	29 Jun 2001	VHF	Alive
157	F	C	16 Jan 2000	11 Jun 2000	VHF	Dropped
158	F	A	16 Jan 2000	29 Jun 2001	VHF	Alive
159	F	C	7 Feb 2000	13 Feb 2000	VHF	Dead
160	F	Y	10 Feb 2001	1 Mar 2001	VHF	Dead
161	F	A	10 Feb 2001	17 Jun 2001	GPS	Alive
162	M	Y	10 Feb 2001	17 May 2001	GPS	Alive
163	M	A	10 Feb 2001	29 Jun 2001	GPS	Alive
164	M	C	11 Feb 2001	11 Jun 2001	VHF	Alive
165	F	A	11 Feb 2001	29 Jun 2001	VHF	Alive
166	M	C	11 Feb 2001	11 Jun 2001	VHF	Alive
167	M	C	11 Feb 2001	29 Jun 2001	VHF	Alive
168	F	C	11 Feb 2001	29 Jun 2001	VHF	Alive
169	M	C	11 Feb 2001	11 Jun 2001	VHF	Alive
170	F	A	11 Feb 2001	11 Jun 2001	VHF	Alive
171	M	C	11 Feb 2001	27 Jun 2001	VHF	Alive
172	M	A	11 Feb 2001	29 Jun 2001	GPS	Alive
173	F	A	12 Feb 2001	22 Jun 2001	VHF	Alive
174	M	C	12 Feb 2001	29 Jun 2001	VHF	Alive

Appendix Table 4. (Continued).

175	F	A	12 Feb 2001	22 Jun 2001	VHF	Alive
176	F	C	12 Feb 2001	29 Jun 2001	VHF	Alive
177	F	A	12 Feb 2001	13 Apr 2001	GPS	Alive
178	F	A	13 Feb 2001	29 Jun 2001	VHF	Alive
179	M	C	13 Feb 2001	22 Jun 2001	VHF	Alive
180	F	A	13 Feb 2001	22 Jun 2001	VHF	Alive
181	F	C	13 Feb 2001	22 Jun 2001	VHF	Alive
182	M	C	13 Feb 2001	11 Jun 2001	VHF	Alive
183	F	C	13 Feb 2001	22 Jun 2001	VHF	Alive
184	F	A	13 Feb 2001	27 Jun 2001	VHF	Alive
185	F	A	13 Feb 2001	4 Jun 2001	GPS	Alive
186	F	A	14 Feb 2001	25 Jun 2001	VHF	Alive
187	F	A	14 Feb 2001	18 Jun 2001	VHF	Alive

[a] A - adult, C - calf, Y - yearling.
[b] GPS - global positioning system, VHF - very high frequency.
[b] Dropped - radio-collar removed by moose.

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