# SURVIVAL, REPRODUCTION, AND MOVEMENTS OF MOOSE IN THE WESTERN UPPER PENINSULA OF MICHIGAN

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ABSTRACT: Moose were extirpated from the Lower Peninsula of Michigan by the late 1800s. Although it is not clear if moose were extirpated from the Upper Peninsula (UP), the population was at the very least, reduced to a low level by ca 1900. Attempts to re-establish a population of moose in the UP during the mid-1930s failed. The Michigan Department of Natural Resources made a second attempt to reestablish moose by translocating animals from Canada to the western UP in 1985 and 1987. Based on optimistic estimates of survival and reproductive rates and habitat surveys, a population of 1,000 moose was expected by the year 2000. However, aerial surveys conducted in the winters of 1996 and 1997 produced population size estimates that were well below 1,000. To determine possible reasons for the slower than expected population growth, 84 moose were outfitted with radio-collars in the winters of 1999-2001. The survival, reproduction, and movements of these moose and 12 others radio-collared in 1995 were monitored from January 1999-June 2001. Overall, 1999-2001 pregnancy rates averaged 75%. Annual adult survival rate (0.88) was higher than yearling survival rate (0.82). First-year calf survival rate (0.71) was high, relative to highly preyed on populations. Annually, approximately 6% of radio-collared moose, primarily yearlings, dispersed out of the study area. The size of moose home ranges was typical of those found in the deciduous/coniferous ecotone of the upper Great Lakes region. Migratory adult moose had larger annual home ranges than did non-migratory adult moose. Low productivity appears to be the likely cause of the slower than predicted population growth. Data from this study can be utilized to facilitate management of moose in the upper Great Lakes region.

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**Key words:** *Alces alces*, dispersal, home range, Michigan, moose, radiotelemetry, reproduction, survival, wildlife translocations

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Prior to extensive European settlement, the eastern sub-species or Taiga moose (*Alces alces americana*) ranged throughout the upper Great Lakes region as far south as the northern Ohio state line (de Vos 1964). In Michigan, moose ranged throughout the state, except for the southwestern portion of the Lower Peninsula (LP) (Wood 1914, Baker 1983). Currently moose are only found in the Upper Peninsula (UP) of Michigan. Moose probably never reached high densities in the LP because habitat quality at the southern periphery of moose range was marginal. Habitat quality probably improved in the northern LP in the mid-1800s because the large forest openings created by widespread logging had begun to regenerate. This improvement was short-lived, however, because vast areas of wildlife habitat were destroyed by the catastrophic firestorms that raged throughout Michigan following the removal of timber (Brewer 1991). Moreover, continued degradation of habitat from expanding human settlement (e.g., conversion of logged-over land to farmland [Whitney 1987]) and unregulated hunting resulted in the extirpation of moose from the LP by the mid-1880s (Wood and Dice 1923). The last credible sighting in the LP 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). To protect the remaining moose in the UP, the Michigan Legislature banned moose hunting in 1899.

Moose persisted longer in the UP because extensive timber harvesting and human settlement did not occur until several decades later than it did in the LP (Hudgins 1953). Despite legal protection, moose numbers dwindled and by the end of the 19th century moose may have been briefly extirpated from the UP. Besides human influences, factors such as wolf (*Canis lupus*) predation and disease, for example, were speculated as contributing to their demise (Verme 1984). The reported poaching of a yearling female in Mackinac County in 1899 is the last documented record of a moose in the UP in the 19th century (Hickie 1944). During the early decades of the 20th century, moose were often reported in the eastern UP (Wood and Dice 1923), however, it is not clear whether these were from a small remnant population or moose that periodically immigrated from Ontario, Canada.

Two attempts were made to reestablish moose in the UP. In the winters of 1935-1937 the Michigan Department of Conservation (MDC) live-trapped and shipped 69 adult moose (32 M, 37 F) from Isle Royale in Lake Superior to several locations in the western UP (WUP) (Hickie 1937, 1944). Sightings of moose increased after these releases, but by the end of World War II the population had again declined. Poor physical condition of the released animals and increased poaching because of food rationing during the war likely contributed to the decline (Verme 1984). The second attempt occurred in January-February 1985 and February 1987 when the Michigan Department of Natural Resources (MDNR) (formerly MDC), in collaboration with the Ontario Ministry of Natural Resources, translocated 58 adult ($\geq$2.5-years of age) and 3 yearling moose (25 M, 36 F; 57 of which survived > 1 week) from Algonquin Provincial Park, Ontario, Canada, to western Marquette County, Michigan. Based on habitat surveys (Wilton 1982) and rudimentary population growth projections, the objective of these translocations was to produce a population of 1,000 moose by the year 2000 (MDNR 1991). Fifteen years after the translocations, moose are still present in the WUP, however the population has not increased as rapidly as expected. Estimates of the population size from aerial surveys conducted in the winters of 1996 and 1997 were 107 and 120 moose, respectively. Also, moose population size estimates for 1996 and 1997 derived from a deterministic population model were both < 500 (1996, $n$ = 452; 1997, $n$ = 494).

Our study was initiated to determine why the moose population in the WUP has not increased as rapidly as anticipated. The objectives were to: (1) determine productivity of moose; (2) estimate sex- and age-specific survival rates of moose; and (3) estimate home range sizes and monitor movements of moose.

## STUDY AREA

The study was conducted in a > 3,000 km$^2$ area in the WUP of Michigan that included portions of Baraga, Dickinson, Iron, and Marquette Counties (Fig. 1). The area was selected because it surrounds the 1985 and 1987 translocation release sites and harbors the greatest known density of moose in the UP. The continental climate of this area is less moderated by the Great Lakes than is the rest of the UP because it is bounded to the south by a large landmass

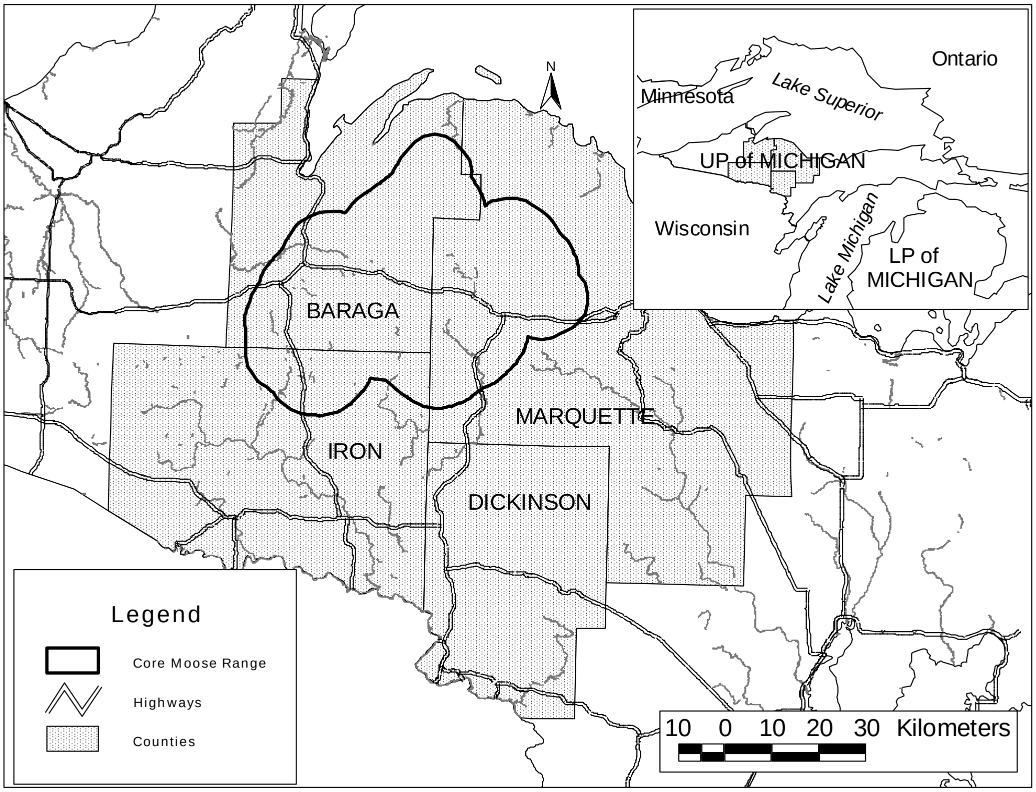



Fig. 1. Moose study area in the western Upper Peninsula of Michigan during Jan 1999-Jun 2001.

(Wisconsin) rather than a large body of water (Lake Michigan). The result is a wider variation in seasonal temperatures, colder winter temperatures, and a greater chance of summer thunderstorms. Annual snowfall ranges from 102 to 356 cm (Eichenlaub 1990). The underlying Precambrian bedrock, most of which is covered with glacial deposits, is part of the Canadian Shield. Soils are mostly acidic because the parent material lacks free lime (McCann 1991). The area lies within the deciduous/coniferous ecotone and is 90% forested, primarily in secondary-growth. Northern hardwood forests lacking American beech (*Fagus grandifolia*), except along the Lake Superior shoreline, dominate upland areas. Drier sites support scattered pines (*Pinus resinosa, P. strobus*) and aspen (*Populus tremuloides, P. grandidentata*). A variety of wetlands occur where bedrock is at or near the surface, including conifer bogs dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*), hardwood swamps dominated by black ash (*Fraxinus nigra*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*), conifer swamps dominated by northern white cedar (*Thuja occidentalis*) and tamarack, and speckled alder (*Alnus incana*) thickets. Moose are classified as a game species (Aho et al. 1995), but are currently not hunted. Potential predators of moose, primarily calves, include black bears (*Ursus americana*) and wolves, however their impact on the population is considered by biologists as negligible. Modern land uses include iron mining, recreation, and timber production.

## METHODS

### Capturing and Radio-Collaring

Moose were captured via net-gunning from a helicopter (Hughes 500 or Bell Long Ranger L-3, Hawkins & Powers Aviation, Inc., Greybull, Wyoming, USA) and fitted with 4-hour motion sensitive radio-collars (VHF: Telonics, Inc., Mesa, Arizona, USA; GPS: Lotek Wireless Inc., Newmarket, Ontario, Canada) in January-February, 1999-2001. We classified moose by sex and identified age (adult, > 2-years of age; yearling, 12-23 months of age; calf, < 12-months of age) based on body size. To minimize stress during capture, moose were blindfolded and their ears plugged with foam rubber. To avoid injury, moose were processed as quickly as possible (average handling time: $\bar{x}$ = 26 min, range = 15-50 min) and their vital signs and behavior were closely monitored.

### Pregnancy Determinations

Blood samples were taken from the jugular vein at time of capture and assays of blood serum for pregnancy-specific protein B (PSPB) (Haigh et al. 1993, Stephenson et al. 1995) were used to determine the pregnancy status of cows. Because PSPB has been shown to reliably detect pregnancy in moose 40 days after conception (Huang et al. 2000), we assumed that cows with detectable levels of PSPB were pregnant. In years subsequent to initial capture, the pregnancy status of cows was determined through assays of fecal material, collected during winter, for fecal progesterone (FP4) levels (Monfort et al. 1993, Schwartz et al. 1995). The FP4 levels of non-pregnant cows were used to establish a 95% upper tolerance limit (FP4-95% UTL) for pregnancy (Messier et al. 1990).

### Radio-Tracking and Monitoring

Radio-collared moose were monitored throughout the study period from a Cessna-172, -182, or -206 aircraft equipped with radio-telemetry tracking equipment (i.e., side-facing, 2-element, Yagi antennas mounted to each wing strut, connected by coaxial cable to a switchbox in the cockpit). Survival monitoring of radio-collared animals was conducted at least once a week and we attempted to obtain at least 2 relocations (radio-fixes) per moose per month. At each relocation we recorded GPS coordinates, time of day, whether the moose was seen, and activity if seen. In addition, all radio-collared cows were approached on the ground in the winter, to collect fecal samples, and during the calving period (15 May-30 Jun [Verme 1984]). Following calving, cows that gave birth were approached on the ground at monthly intervals to assess survival of their calves.

### Survival

Annual (1 Jun-31 May), summer (1 May-31 Oct), and winter (1 Nov-30 Apr) survival rates (with 95% CIs) were estimated for adults, yearlings, cows (adult females), and bulls (adult males) using MICROMORT (Heisey and Fuller 1985), which incorporates the Mayfield survival estimator (Mayfield 1961, 1975; Trent and Rongstad 1974). Survival monitoring of moose radio-collared in 1999 began on 1 May; thereafter animals entered the study on the day they were radio-collared (i.e., staggered entry [see Pollock et al. 1989]). To accommodate staggered entry and meet the constant survival assumption of the Mayfield estimator, the biological year was divided into monthly intervals with a constant weekly survival rate. Period survival rates were then equal to the product of the monthly survival rates (e.g., $\hat{S}_{winter} = \hat{S}_{Nov} \times \hat{S}_{Dec} \times \ldots \times \hat{S}_{Apr}$). Censored animals (i.e., those from which radio signal contact was lost) were included in survival analysis up to the point at which they were censored (Vangilder and Sheriff 1990).

Date of death (or censoring) was estimated at halfway between the last recorded live signal and the date that the moose was first known to be dead (or censored).

First-year, 0-6 month (~1 Jun-30 Nov), and 7-12 month (~1 Dec-31 May) survival rate estimates were calculated jointly for radio-collared calves and un-collared calves of radio-collared cows. Calves not seen in the spring that were subsequently radio-collared during their first winter were not included in calf survival analysis. Survival monitoring of un-collared calves began the day they were first observed. Because survival monitoring of un-collared calves occurred once a month, all calves were assumed to have a constant monthly survival rate. A calf was considered to have died if its cow had either died or was found alone for two consecutive months prior to the calf attaining 8-months of age (the earlierst age of known cow-calf separation). Dead calves were assigned the date of death of their cow or the date halfway between the last date the calf was seen with its cow and the date the cow was first seen alone.

### Home Range and Movements

Annual (1 May-30 Apr), summer, and winter home ranges of adult moose were determined with the Animal Movement Analyst Extension (AMAE; Hooge et al. 1999) to ArcView® (Environmental Systems Research, Inc., Redlands, California, USA) Geographic Information System (GIS). The 95% utilization distribution (UD) of the fixed kernel (FK; Worton 1989) was used to estimate home range sizes. The smoothing factor was calculated via least squares cross validation (LSCV). Home range size estimates were determined only when > 18 relocations annually and > 9 relocations per season were available. Because a minimum of 30 relocations per animal is recommended to accurately estimate home range area with the FK method when LSCV is used, our results likely overestimate moose home range sizes (Seaman et al. 1999). Radio-fixes that deviated from grouped relocation points were considered transitory, and were not included in home range estimates. Moose were classified as migratory if < 25% of their seasonal home ranges overlapped and there was $\geq$ 2 km between the center of the FK 25% UD of their seasonal home ranges. Because the use of GPS radio-collars was experimental, home range sizes were determined only for moose with VHF radio-collars.

Annual dispersal rates (with 95% CIs) were estimated using MICROMORT (Heisey and Fuller 1985). A moose was considered to have dispersed if it permanently emigrated > 30 km straight line from its capture location or previous home range. This distance was chosen because it was greater than the maximum distance (26 km) a migratory moose moved between seasonal home ranges.

### Data Analysis

The Mann-Whitney U-test was used to make comparisons between FP4 concentrations of pregnant and non-pregnant cows and among home range size estimates. Comparisons between survival estimates where made with a Z-test statistic (Pollock et al. 1989) when > 25 moose per treatment (e.g., age, sex) were available (Winterstein et al. 2001). Unless otherwise noted, significance level for all statistical analyses was $\alpha = 0.05$.

## RESULTS

### Capturing and Radio-collaring

Thirty-four adults (32 F, 2 M), 4 yearlings (4 F), and 36 calves (13 F, 23 M) were captured and radio-collared with standard VHF collars. In addition, GPS collars were placed on 4 adult moose (2 F, 2 M) in 2000 and 5 adult moose (2 M, 3 F) and one yearling (1 M) in 2001. Twelve adult moose (6 F, 6 M) that were radio-collared in 1995 were also part of the initial sample population. No moose died or were injured during capture and no signs of capture myopathy (e.g., muscle stiffness, lethargy) were observed following capture in any year.

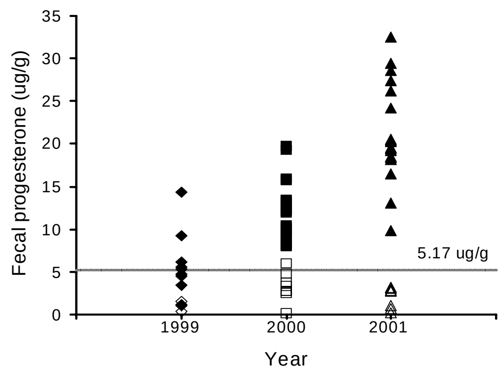
**Radio-Tracking and Monitoring**

During Feb 1999-Jun 2001, we conducted 195 radiotracking flights and recorded 2,384 relocations of radio-tagged moose. Moose with VHF radio-collars were relocated an average of 1.75 times per month whereas those with GPS radio-collars were relocated 1.50 times per month. More aerial observations of radio-tagged moose were made per flight in the winter ($\bar{x}$ = 5.04, range = 0-30) than in the summer ($\bar{x}$ = 1.15, range = 0-11). Radio-tagged cows were relocated on the ground an additional 312 times, during which 281 observations of moose (183 cows, 98 calves) were made. Cows were approached between 0900 and 2300 hours, however, 87% of approaches occurred after midday.

**Pregnancy Determinations**

Sixty-nine percent (25 of 36) of captured cows from which useable blood serum samples were collected had detectable PSPB levels indicating pregnancy. Mean and median PSPB concentrations pooled across 2000-2001 were 411.05 ± 69.38 (SE) and 387.30 ng/mL, respectively (1999 PSPB values were unavailable because PSPB results were reported as positive or negative only). We collected 111 fecal samples (36 at capture, 75 post capture) from 41 cows. Multiple fecal samples were collected from 18 cows in 2000 ($\bar{x}$ = 2.18) and 19 cows in 2001 ($\bar{x}$ = 2.05). FP4 concentrations fell into fairly distinct pregnant and non-pregnant groups each year, although the results were not unequivocal (Fig. 2). Pooled

Fig. 2. Progesterone concentration in fecal material collected in winter from radio-collared cow moose during 1999-2001 in the western Upper Peninsula of Michigan. Each symbol represents the mean fecal progesterone concentration of a single moose. The 95% upper tolerance limit (95% UTL; horizontal line) between pregnant (◆, ■, ▲) and non-pregnant (◇,□, △) cows was 5.17 mg/g.




mean ± SE and median values for pregnant cows were 16.29 ± 0.98 and 14.46 mg/g, whereas for non-pregnant cows the values were 2.30 ± 0.32 and 2.66 mg/g, respectively. FP4 concentrations of pregnant cows were significantly different from those of non-pregnant cows (Mann-Whitney U test, $Z_{MWU}$ = -7.1730, $P$ < 0.0001). The FP4-95% UTL for pregnancy was 5.17 μg/g of dried feces. Retroactively applying the FP4-95% UTL to the average FP4 levels of individual cows, 92% (44 of 48) of pregnant cows (i.e., those with positive PSPB results and/or that gave birth) and 94% (17 of 18) of non-pregnant cows would have been correctly identified. The average annual pregnancy rate (adjusted for cows for which pregnancy test results were not available, but that were observed with calves) was 74% (Table 1).

**Reproduction**

Of the pregnant cows (i.e., those with positive PSPB or positive FP4 results, or

Table 1. Productivity of radio-collared adult cow moose studied during 1999-2001 in the western Upper Peninsula of Michigan.

| Year | No. cows | % cows pregnant[1] | % cows reproducing | No. calves produced | % twins | Spring calf : cow | Year end calf : cow |
|---|---|---|---|---|---|---|---|
| 1999-00 | 18 | 78 | 78 | 19 | 36 | 1.06 : 1 | 0.76 : 1 |
| 2000-01 | 27 | 70 | 67 | 19 | 6 | 0.70 : 1 | 0.60 : 1 |
| 2001-02 | 41 | 76 | 59 | 29 | 21 | 0.71 : 1 | - |
| $\bar{x}$ or total | 86 | 74 | 65 | 67 | 19 | 0.78 : 1 | 0.72 : 1 |

[1]Cows with positive PSPB or FP4 results, plus cows for which pregnancy tests were not available, but were observed with calves in the spring.

Note: year-end calf:cow for 2001-02 unavailable; study ended 30 June 2001.

that reproduced if pregnancy test results were not available), 78% (14 of 18) in 1999, 67% (18 of 27) in 2000, and 59% (24 of 41) in 2001 were observed with at least 1 calf in the spring (Table 1). Overall, adult cows produced 19 calves in 1999 and 2000, and 29 calves in 2001. The earliest visual confirmation of calving was 21 May in 1999, 24 May in 2000, and 15 May in 2001. Frequency of twinning varied from 6% to 36% ($\bar{x}$ = 19%). Post-calving calf:cow ratios (Table 1) decreased from 1.06 in 1999 to 0.70 in 2000 and remained relatively unchanged in 2001 (0.71). Due to the loss of a greater number of calves than cows, calf:cow ratios decreased 28% during 1999-2000 and 14% during 2000-2001 (Table 1). The year-end calf:cow ratio for 2001-02 was not available because the study ended. During the study, only 1 yearling female reproduced, giving birth to a single calf in 2000. Among the remaining 9 yearling females, 3 had negative PSPB results, 3 were observed alone during spring natality checks, and 3 were unknown as regards to calving.

### Survival

Of 96 moose (60 F, 36 M) that were monitored, 72 (46 F, 26 M) were known to be alive at the end of the study, 4 (2 F, 2 M) shed their radio-collars, 4 (2 F, 2 M) had their GPS radio-collars removed to collect the data stored in each collar (the GPS radio-collar of 1 male was replaced with a VHF radio-collar), and 17 (11 F, 6 M) died. Three (2 F, 1 M) deaths were attributed to cerebrospinal nematodiasis (*Parelaphostrongylus tenuis*). One male was killed by a motor vehicle and wolves killed a yearling female. Eight (47%) moose that died were also heavily parasitized by the large American liver fluke (*Fascioloides magna*). Three (1 F, 2 M) moose that died during the winter had < 20% femur marrow fat (dry weight) indicating severe malnutrition (Peterson et al. 1984). However, all 3 had additional maladies (e.g., *P. tenuis* and/or *F. magna*) that likely contributed to their deaths. Other causes of death included accidents, birthing complications, and old age. Ages of dead moose, estimated by counting cementum annuli of sectioned first incisors, excluding calves, ranged from 1.0 to 13.0 years for females ($\bar{x}$ = 4.75 ± 1.24, $n$ = 10) and 1.5 to 7.5 years for males ($\bar{x}$ = 3.0 ± 1.12, $n$ = 5).

Annual survival of adults did not differ ($Z$ = 0.089, $P$ = 0.465) between 1999-00 ($\hat{S}$ = 0.880) and 2000-01 ($\hat{S}$ = 0.873). Also, although more adults died in the winter ($n$ = 7) than in the summer ($n$ = 4) no difference was found between winter and summer survival rates of adults in either year (1999-00: winter $\hat{S}$ = 0.934, summer $\hat{S}$ = 0.966, $Z$ = -0.554, $P$ = 0.301; 2000-01: winter $\hat{S}$ = 0.913, summer $\hat{S}$ = 0.933, $Z$ = -0.357, $P$ = 0.364). In 1999-00, annual survival of bulls ($\hat{S}$ = 1.000) was 16% higher than that of cows ($\hat{S}$ = 0.840), whereas in 2000-01, annual survival of cows ($\hat{S}$ = 0.882) was 2% higher than that of bulls ($\hat{S}$ = 0.857). The small sample of radio-collared bulls in 1999-00 ($n$ = 9) was probably the reason that survival of bulls was so high that year. Survival rates of cows, between years (1999-00 $\hat{S}$ = 0.840, 2000-01 $\hat{S}$ = 0.882, $Z$ = -0.449, $P$ = 0.335) and between winter and summer in 2000-01 (winter $\hat{S}$ = 0.911, summer $\hat{S}$ = 0.937, $Z$ = -0.398, $P$ = 0.351) were not significantly different. Annual survival of yearlings was lower than that of adults in 1999-00 (yearling $\hat{S}$ = 0.840) and 2000-01 (yearling $\hat{S}$ = 0.800). In 1999-00, survival rates of yearlings between summer and winter were only slightly different (0.914 vs. 0.919), whereas, in 2000-01 summer survival of yearlings was 6% greater than in winter (0.924 vs. 0.867).

Seventy percent (7 of 10) of calf deaths occurred in the winter. This seasonally skewed calf mortality pattern, however, could be a result of the frequency (monthly) at which calf survival was checked and the difficulty of detecting calves that died shortly after birth. First-year survival of calves in 1999-00 was 20% lower than that in 2000-01 (Table 2). Sixty-seven percent (4 of 6) of calf mortalities in 1999-00 and 25% (1 of 4) in 2000-01 occurred within the first six months of life. Calf survival from 0-6 months was 20% lower in 1999-00 than in 2000-01. Thirty-three percent (2 of 6) of calf mortalities in 1999 and 75% (3 of 4) in 2000 occurred between 7 and 12 months of age. Seven to twelve month calf survival did not differ from 1999 to 2000.

### Home Range and Movements

In 1999-00, 22% (4 of 18) of adults migrated between distinct summer and winter home ranges, while in 2000-01, 38% (14 of 37) of adults migrated seasonally. Migration distance ranged from 2 to 26 km ($\bar{x}$ = 11 km). The median date of arrival on summer home range was 22 May and on winter home range it was 13 October. Home range sizes (Table 3) of migratory adults did not differ between winter and summer ($Z_{MWU}$ = -1.5615, $P$ = 0.118). Annual home ranges of migratory adult moose were larger ($Z_{MWU}$ = 2.4664, $P$ = 0.014) than those of non-migratory adult moose. No differences were detected between home range sizes of cows and bulls ($Z_{MWU}$ = 0.0102, $P$ = 0.992). Although, cows attended by calves had

Table 2. First-year, 0-6 month, and 7-12 month 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.

| Year | Category | $\hat{S}$ [1] | No. calves | No. months | No. deaths | 95% LCI | 95% UCI |
|---|---|---|---|---|---|---|---|
| 1999-00 | First-year | 0.634 | 17 | 157 | 6 | 0.439 | 0.915 |
| | 0-6 month | 0.754 | 17 | 87 | 4 | 0.568 | 0.988 |
| | 7-12 month | 0.840 | 13 | 70 | 2 | 0.657 | 1.000 |
| 2000-01 | First-year | 0.787 | 20 | 203 | 4 | 0.622 | 0.995 |
| | 0-6 month | 0.943 | 20 | 102 | 1 | 0.838 | 1.000 |
| | 7-12 month | 0.835 | 19 | 101 | 3 | 0.678 | 1.000 |

[1]Mayfield estimator (Mayfield 1961, 1975; Trent and Rongstad 1974).

Table 3. Annual and seasonal home range sizes of migratory and non-migratory adult moose, bulls, cows, cows attended by calves, and cows not attended by calves during 1999-2001 in the western Upper Peninsula of Michigan.

| Season | Category | No. moose | No. locations | Mean ($km^2$) | Median ($km^2$) | SE | Range ($km^2$) |
|---|---|---|---|---|---|---|---|
| Annual | Migratory | 18 | 20-30 | 63 | 53 | 7.12 | 20-122 |
| | Non-migratory | 37 | 19-34 | 43 | 41 | 3.49 | 14-99 |
| | Bulls | 12 | 19-24 | 47 | 43 | 5.97 | 22-80 |
| | Cows | 43 | 20-34 | 50 | 44 | 4.19 | 14-122 |
| | Cows w/calves | 29 | 21-34 | 48 | 44 | 5.19 | 14-115 |
| | Cows w/out calves | 11 | 20-28 | 51 | 49 | 6.01 | 25-96 |
| Summer | Migratory | 16 | 11-24 | 44 | 39 | 6.04 | 9-98 |
| Winter | Migratory | 8 | 10-15 | 27 | 23 | 7.58 | 3-64 |

smaller home ranges than did solitary cows, the differences were not significant ($Z_{MWU}$ = 0.6664, $P$ = 0.505).

Five yearlings (3 M, 2 F) and 1 adult cow permanently dispersed a mean linear distance of 80 ± 16 km (SE) (range = 30-134 km) during the study. The 2 yearling females, 1 yearling male, and the cow dispersed during April-June. The other 2 yearling males dispersed in January and September, respectively. The estimated annual dispersal rate was 0.068 (CI, $0.000 \leq 0.068 \leq 0.139$) in 1999-00 and 0.054 (CI, $0.000 \leq 0.054 \leq 0.122$) in 2000-01.

## DISCUSSION

### Pregnancy Determination and Productivity

PSPB and FP4 appeared to be accurate at determining pregnancy. However, 27% (6 of 22) of cows with positive PSPB test results were not observed with calves during the spring. Four of these cows also had fecal progesterone levels greater than the FP4-95% UTL for pregnancy (5.17 μg/g). Although each of these cows was approached 2-3 times, it is possible that we did not find a calf (calves) because it (they) died shortly after birth or within the interval between cow sightings. No cows with negative PSPB results were observed with calves. In addition, using PSPB results as a baseline, FP4 test results would have correctly identified 83% of pregnant and 90% of non-pregnant cows.

Adult pregnancy rates in the WUP were relatively constant from year to year (CV = 4.72%), but were lower than the 84.2% average reported by Boer (1992) for moose in North America. Stenhouse et al. (1995) also reported higher pregnancy rates than were found in the WUP. In western Northwest Territories where moose densities are low (0.14 - 0.16 moose/$km^2$), the pregnancy rate of adult females was 96% (Stenhouse et al. 1995). In contrast, adult pregnancy rates in the WUP, where moose also occur at low density (0.29 moose/$km^2$) (MDNR, unpublished data), were higher than those found by Cox et al. (1997) in northwest Minnesota where moose populations have been in decline. For example, at Agassiz National Wildlife Refuge (ANWR) where the population had decreased 62% during 1993-1994 (0.50 moose/$km^2$ to 0.31 moose/$km^2$), the average adult pregnancy rate during 1995-1997 was 37.5% (Cox et al. 1997). In addition, at Beltrami Island State Forest (BISF), where moose had apparently been declining for decades (1971: 0.54 moose/

$km^2$ - 1996: 0.07 moose/$km^2$), Cox et al. (1997) reported that only 51% of cows were pregnant. Our results and those from western Northwest Territories and northwest Minnesota differ from that of Boer (1992) who found that adult pregnancy rates were quite similar across a wide range of population densities, as well as geographic areas, winter severities, and habitats. However, pregnancy rates per se, may not be the best index of moose productivity. Adult twinning rates and yearling pregnancy rates, the variable components of fecundity (Boer 1992), are likely better indicators of moose productivity (Aitken and Child 1992)

Although few yearling females were radio-collared in any 1 year ($\bar{x}$ = 3), the mean annual pregnancy rate for yearlings(< 9%) was low compared to the North American average of 48.7% reported by Boer (1992). Twinning rates were comparable to those found by Blood (1974) in Alberta, Canada (range = 4-48%). However, the mean twinning rate was below that reported by MDNR biologists in the WUP during 1985-1995 (Aho et al. 1995; 36%) and by Boer (1992; 33.3%). Frequency of twinning has been shown to be a good indicator of cow health condition and habitat quality. On the Kenai Peninsula, Alaska, 70% of cows living on high quality habitat gave birth to twins, whereas only 20% living on poor quality habitat did so (Franzmann and Schwartz 1985). Furthermore, Boer (1992) found a direct relationship between adult twinning rates and yearling pregnancy rates. Therefore, these measures of productivity are likely influenced by the same habitat component. However, no study has yet quantitatively related habitat quality and availability to moose productivity (Crête and Courtois 1997).

Finally, it has been suggested that at low population density a low bull:cow ratio may affect breeding of cows and productivity (Crête et al. 1981, Albright and Keith 1987). This does not appear to be a problem in the WUP where bulls, on average, comprised 50% of the adult winter population during 1999-2002 (MDNR, unpublished data).

**Survival**

Adult and yearling survival rates were similar to those reported for other non-hunted, lightly preyed on, moose populations. For example, in Alberta, Canada, Mytton and Keith (1981), reported mean annual survival rates of 0.86 for adults and 0.83 for yearlings. Also, in a newly established moose population in southwest Colorado, Olterman and Kenvin (1998) reported slightly higher bull survival (0.94, >1%) and a slightly lower cow survival (0.83, <2%) than were found in this study. Furthermore, mean annual cow survival was 28% and 19% higher than that reported by Cox et al. (1997) at ANWR (0.67) and BISF (0.72), respectively.

The relatively high survival rate of calves in the WUP suggests that predation is not a significant mortality factor. First-year calf survival rates were similar to those in Alberta, Canada (0.67; Mytton and Keith 1981) and higher than those in northwest Minnesota (0.56; Cox et al. 1997), both areas where predation of neonates is low. This contrasts with studies in Alaska and Canada where bears and wolves often kill substantial numbers of calves. In south-central Alaska, brown bear (*Ursus arctos*) predation accounted for 73% of all calf deaths and survival of calves $\leq$ 5-months of age was only 0.39 (Ballard et al. 1991). Also, in northeastern Alberta, Hauge and Keith (1981) reported an annual calf mortality rate of 73%, of which 29% was attributed to wolf predation.

**Home Range and Movements**

The proportion of seasonally migratory moose in the WUP (20-40%) was similar to that reported by Addison et al. (1980) in northwest Ontario, Canada (27%), and Phillips et al. (1973) in northwest Minnesota (20%). The distance between summer and winter home ranges was also comparable to those reported by Addison et al. (1980) in northwest Ontario ($\bar{x}$ = 7 km, range = 2-13 km) and Phillips et al. (1973) in northwest Minnesota ($\bar{x}$ = 16 km, range = 14-34 km). In contrast, migration distances were smaller than those found by Ballard et al. (1991) in interior south-central Alaska, ($\bar{x}$ = 48 km, range = 10-68 km) and Mauer (1998) southeast of the Brooks Range in Alaska and Canada ($\bar{x}$ = 123 km, range = 18-196 km).

Because of the different methods (e.g., minimum convex polygon, probabilistic) used to estimate home range size and other difficulties (e.g., sample size, delineation of seasons, etc.), it is problematic to make comparisons among different studies. Nevertheless, in general, moose home ranges were comparable in size to those found for moose in the upper Great Lakes region. For a more detailed comparison of home range sizes from different geographic locations in North America see Hundertmark (1998:316-317).

Five of twenty-six (19%) offspring permanently dispersed out of the core study area shortly after separation from their cows. In south-central Alaska, Ballard et al. (1991) reported that 33% of offspring fully dispersed from their natal home range, and that more males than females dispersed. Although we did not observe a male biased dispersal, all moose that dispersed except 1, were yearlings. In central Alberta, Canada, Lynch (1976) found that 50% of subadults (< 2-years of age) and 17% of adults dispersed. These values are probably overestimates however, because he considered moose from which radio contact had been lost to have dispersed. In the WUP, Aho et al. (1995) reported that a yearling female and a yearling male emigrated at least 160 km to Wisconsin over a 9-month (Mar 1989-Dec 1990) and 7-month (Mar-Oct 1994) period, respectively.

## CONCLUSIONS

Although moose in the WUP appear to be well established, biologists believe that the population is below carrying capacity. Based on a Habitat Suitability Index (HSI) model (Model 2; Allen et al. 1987) cover-type composition variables, Patterson et al. (1995) estimated that suitable habitat in Baraga county (1,073 $km^2$) could support 1.72 moose/$km^2$. By comparison, on 25 plots (16 of which wholly or partially fell within Baraga county [total area = 1,549 $km^2$]) designated as having high moose density, preliminary mark-resight population estimates for winter 2002 were 0.29 moose/$km^2$ (MDNR, unpublished data). This > 6-fold difference between potential habitat carrying capacity and the estimated population size suggests that further growth of the moose herd in the WUP is possible.

The relatively high survival of all age categories indicates that moose are probably in good physical condition and that disease and predation are not limiting population growth. In addition, the size of moose home ranges and their seasonal movement patterns indicate that there is good interspersion and juxtaposition of suitable habitat types. Low productivity appears to be the primary reason the moose population in the WUP has not increased as rapidly as expected. Because productivity is dependent on female body condition which, in turn, is directly related to food supply (Franzmann and Schwartz 1985), one possible explanation then, is that the quality, quantity, and availability of food is less than optimal for maximum productivity.

Additionally, because moose in the WUP are at the southern extent of their range in eastern North America, the environmental conditions (e.g., climate) that have prevented further range expansion have also likely played a role in limiting population growth.

## MANAGEMENT IMPLICATIONS

Our results suggest that low productivity, exhibited in below average adult pregnancy rates and low production of twins, coupled with nearly non-existent yearling reproduction, is an important reason the population has not increased as predicted. In retrospect, the original population objective of 1,000 moose 15 years after the 1985 translocation was overly optimistic. A reevaluation of this objective is warranted. In addition, a closer examination of the potential of moose habitat in the upper Great Lakes region through a quantitative assessment of the nutritional quality and availability of forage is suggested. Furthermore, monitoring the survival and movements of moose, the collection and analysis of fecal samples for FP4, which has been shown to be a reliable indicator of pregnancy, and determination of spring calf production should be continued for several years. The information obtained by further study will assist wildlife managers of reintroduced and/or small moose herds to set realistic population objectives.

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