INTEGRATING HABITAT USE AND POPULATION DYNAMICS OF MOOSE IN NORTHERN NEW HAMPSHIRE

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ABSTRACT: The New Hampshire Fish and Game Department and the University of New Hampshire initiated research in northern New Hampshire to better understand population dynamics and seasonal habitat use of a moose population that has apparently stabilized, despite optimal habitat and modest harvest levels. In total, 94 moose were captured by helicopter (81 net-gunned and 13 tranquilized) in December 2001-2003 and 2 were darted at salt-licks in July of 2002. Capture mortality attributed to myopathy and injury was 4%. In comparison to measured reproduction during capture (63 and 100%), our ability to measure pregnancy by direct observations (69 and 100%) was validated in 2002-2003. Production was 0.82 and 0.85 calves per adult cow; rate of twinning was 20 and 10%. Calf mortality 2 months post-partum was similar (26 and 27%) each year. Annual mortality of adult/yearling moose was 27 and 12%. Hunting and vehicle collision mortality was 4 (all adult cows) and 6% (all calves but 1) each year. High annual winter calf mortality (38-43%) in late March and early April was associated with the combined effects of malnutrition and winter tick/lung nematodes. Winter home range size was not restricted, and composition of available habitat was similar across seasons although overlap was minimal between seasons. Consideration of habitat and population dynamics data suggests that both density dependent and independent factors could be influencing the study population.

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Moose (*Alces alces*) have become an extremely valuable resource in northern New Hampshire in the past 20 years. Moose watching tours and casual visitation of moose viewing areas (predominantly road-side salt licks) by tourists provide measurable economic and recreational benefit in the region (Silverberg 2000). Revenue derived from hunting permits increases annually and fuels other hunting related purchases (Bontaites and Gustafson 1993). Because of the significant recreational and economic importance of the moose population, and the direct relationship of herd health to commercial forest management, it is important to manage this population with the best scientific information. However, moose research in the northeastern United States is limited in scope and extent. Specifically, only a 2-year study (Miller 1989) with marked moose has addressed habitat use in New Hampshire.

Population indices derived from deer hunter surveys, road collisions, and infrared aerial surveys suggest that New Hampshire's northern moose population has approached stability, despite perceived high quality and quantity of suitable habitat and modest harvest levels (K. Bontaites, New Hampshire Fish and Game Department, unpublished data). It is presumed that substantial non-hunting mortality of unknown sources occurs in the population. Mortality and survival rates, rate

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of production, and habitat use are fundamental parameters in understanding moose population dynamics (Van Ballenberghe and Ballard 1998). However, habitat use and life history of moose in New England are different from that in much moose range, and population dynamics has not been extensively researched in this region. Seasonal home range and habitat use were measured in northern New Hampshire (Miller 1989) and Maine (Thompson et al. 1995) previously, however, both studies were relatively short-term.

The overall objective of this study was to measure seasonal home range and habitat use, productivity, and rate, timing, and cause of mortality of cow and calf moose for 4 continuous years. This paper highlights population dynamics and habitat use data collected in December 2001-2003, and evaluates the efficiency of capturing free-ranging moose from a helicopter.

STUDY AREA

The study area was in eastern Coos County in northern New Hampshire (Fig. 1) encompassing approximately 650 km^2 of rolling to mountainous, forested terrain. The study area includes numerous ponds and lakes, with the Androscoggin River located centrally within. The majority of the study area is working commercial forestland. Dominant forest types include northern hardwoods (34%) as a mix of yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*) on more well drained sites (Degraaf et al. 1992). On more poorly drained sites, spruce-fir forests are common (23%), consisting almost entirely of red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*). Approximately 17% of the study area was mixed forest, typically including yellow and paper birch (*Betula papyrifera*) and either balsam fir or red spruce. Other important communities included clearcuts and regeneration stands (14%) of aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) where pin cherry (*Prunus serotina*) was common. Tamarack (*Larix laricina*) and northern white cedar (*Thuja occidentalis*) were found on very poorly drained soils. Wetlands, including open water, accounted for 10% of the total study area. Mean weekly snow depth measured at fixed sites within the project area was < 50 cm in 2002 and 42.6 cm (8-70 cm) in 2003. Seasonal temperatures range from < -30 to > +30˚C. Predators in the study area included black bears (*Ursus americana*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*); white-tailed deer (*Odocoileus virginianus*) were sympatric with moose throughout the area. Both sexes of moose are hunted annually by a permit-lottery system; hunter success rates typically exceed 85% (NHFG 2002).

METHODS

Moose were captured from a helicopter with net-guns (*n* = 81, Carpenter and Innes 1995) or tranquilizers (*n* = 13) in December 2001-2003, and subsequently fitted with a VHF or GPS radio collar (VHF: Model 600, GPS: Model TGW-3700, Telonics, Inc., Mesa, Arizona, USA). Moose were tranquilized with a mixture of carfentanil citrate and xylazine hydrochloride and were antagonized with a mixture of naltrexone hydrochloride and tolazoline hydrochloride given intravenously. Respiration and temperature were monitored by a veterinarian. Approximately 20 mL of blood, fecal pellets, and hair and parasite samples were collected from each moose. Certain moose, typically adults, were tranquilized from the helicopter in 2001 because the lack of snow cover affected the ability of the pilot to identify snags/branches that could snag the net or rotors. Spotter planes were used to help locate potential target moose in 2002 and 2003.

The primary capture goal varied each year to ensure that 25 adult cows were available for productivity measurements each spring. The capture targets were 25 cows and 15 calves

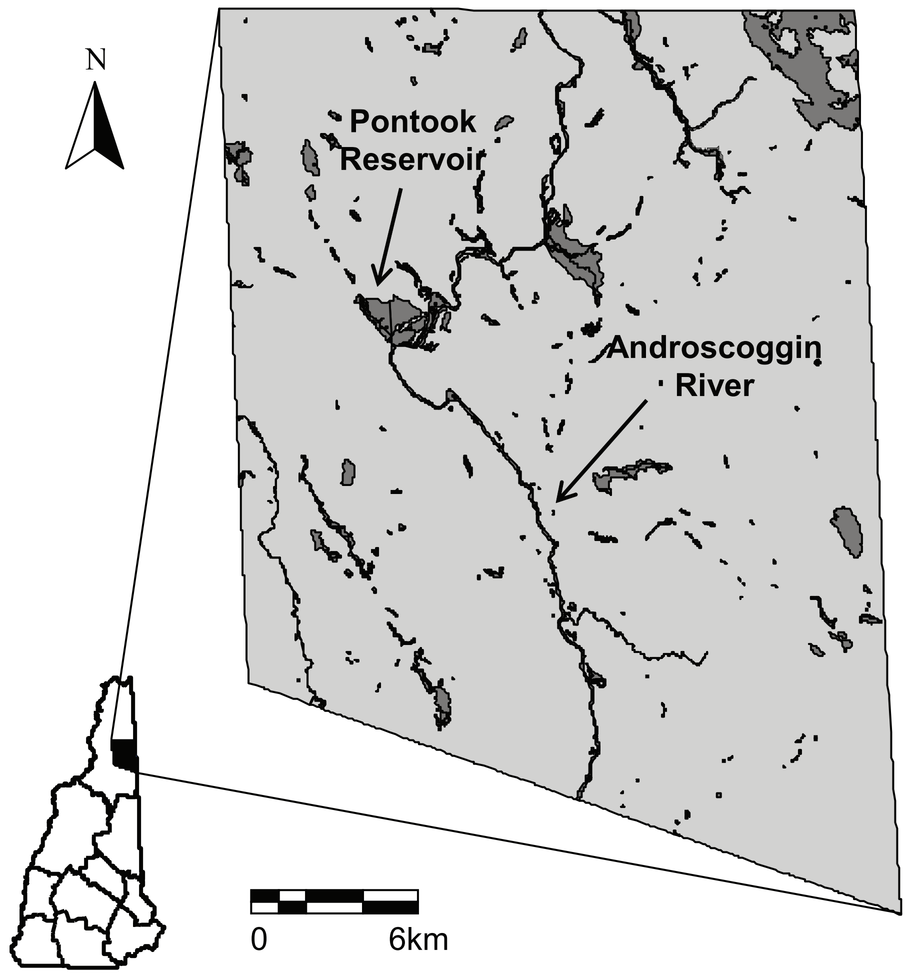

Fig. 1. Study area located in eastern Coos County, New Hampshire, USA.

in 2001, 4 cows and 21 calves in 2002, and 1 cow and 25 calves in 2003. All non-calves captured were considered adult; identification of calves was not problematic. In July 2002, 2 adult cows were tranquilized at a salt lick to redeploy GPS collars.

Radio collared moose were located by aerial and ground-based telemetry methods (Mech 1983) 1-3 times weekly year-round, or by direct observation during spring-summer as described below. Ground-based telemetry was performed with TR-5, TR-3, TR-2 digital and analog receivers (Telonics, Inc., Mesa, Arizona, USA) and 3-element Yagi directional antennas (AF Antronics, Inc., Urbana, Illinois, USA). Because moose travel extensively at night during summer, monitoring occurred evenly in 4 discrete time periods to avoid bias associated with diurnal only sampling (Beyer and Haufler 1994). Time periods were defined as follows: feeding (0300–0900 hours), bedding (0900–1500 hrs), feeding (1500–2100 hrs), and salt lick use (2100–0300 hrs). Dead moose, as indicated by mortality sensors, were located within 48 hours and a field necropsy was performed to determine the probable cause of death.

Pregnancy of cows captured in 2001 was measured with moose pregnancy-specific protein B in blood samples (Huang et al. 2000), and with a portable ultrasound unit in 2002 (Stephenson et al. 1995). Beginning 1 May, close observation of adult cows was attempted 2-3 times weekly to document production, fecundity, and calf survival/mortality for 2 months post-partum. Those cows believed barren were observed weekly through July to identify late births. Technicians used homing techniques (Mech 1983) to stalk adult cows within sighting distance to identify the presence and number of calves. Annual mortality rates of all moose were calculated each calendar year (2002: n = 28, 2003: n = 47); moose with dropped collars were precluded from this analysis. Calf winter (1 December – 1 May) mortality rates were calculated from observations of radio-collared calves (approximately 7 months old) following capture in 2001-2003. Because 8 of 14 radio-collared calves dropped collars in winter 2002 following capture and the remaining 6 died, reported winter mortality in 2002 represents a minimum mortality rate.

Telemetry data and locations from visual observations were recorded with handheld GPS units (Garmin, Miami, Florida, USA). Triangulation data were recorded in Universal Transverse Mercator (UTM) coordinates and analyzed with the LOCATE II program (Nams 2000), which utilizes maximum likelihood estimators (Lenth 1981) to estimate locations (≥ 3 directional bearings per location). Telemetry error was estimated from a radio-collar at known locations.

Telemetry locations were used to construct annual and seasonal 95% minimum convex polygon (MCP, Mohr 1947) home ranges using the Floating Amean method (Rodgers and Carr 1998). Seasons were defined as winter (16 December–15 April), spring (16 April–15 June), summer (16 June-15 September), and fall (16 September–15 December). Locations were plotted and analyzed with ArcView™ Geographic Information System (GIS) 3.3 (ESRI, Redlands, California, USA) and HRE: The Home Range Extension for ArcView™ (Rodgers and Carr 1998). Seasonal core areas were defined as 70% seasonal MCP. Number of locations was plotted against mean home range size to evaluate if correlation existed.

Cows that were monitored for 2 consecutive years and were observed with a newborn calf each year (n = 9) were included in the home range analysis. This increased statistical power by accounting for variability between moose and years. Percent overlap was calculated as the proportion of the overlapped area between 2 seasons divided by the total area encompassed by the 2 seasonal ranges. Proportional data form a binomial distribution, thus percent overlap was arcsine transformed to allow use of parametric statistics (Zar 1999), though data presented are actual proportions. Analysis of variance (ANOVA) was used to examine for differences in mean seasonal home range size, overlap, and percent overlap; moose and year were blocking factors. Pairwise comparisons were made with Tukey's test. Significance for all tests was assigned a priori at $\alpha = 0.05$.

The proportion of 6 major habitat types within annual and seasonal home ranges, and seasonal core areas of 10 reproductive cow moose were calculated in 2002. Limitations of cover classification in certain home ranges and sample size prevented comparisons in multiple years. Forest cover types interpreted from GRANIT 2001 Landcover Assessment were grouped into 6 categories characterized by the dominant vegetation; northern hardwood (< 25% coniferous basal area per acre), coniferous (> 65% coniferous basal area), mixed (> 25% and < 65% coniferous basal area), wetland, cut-regeneration, and developed/other (includes agricultural land, residential and commercial housing, and bedrock). Due to statistical issues of non-independence and 0-values, the proportion of available habitat was not statistically analyzed, but rather was used as an overall indication of home range composition and compared across seasons.

RESULTS

Captures

Capture targets were met each year in conditions ranging from minimal to >75 cm snow depth. The capture rate ranged from 6-17 moose daily with captures spread throughout the day. The highest capture rates were in 2003 when calves were targeted (24 of 25 targeted animals), snow depth was greatest, and a spotter plane helped locate moose for the helicopter crew. Only 1 of 94 moose escaped without being collared during the helicopter capture procedure. Mortality (all calves) during or associated (myopathy within 6 days) with capture was 4% (4 of 94). The composition of captured moose was 31 yearling/adult cows and 63 calves (31 female and 32 male). The rate of pregnancy measured in 2001 and 2002 was 63 (15 of 24) and 100% (4 of 4). Eight calves dropped their collars in late winter 2002.

Population Dynamics

Calves were observed with 15 of 22 (68%) cows and 20 of 26 (77%) cows monitored in spring 2002 and 2003. Neonates were observed from 14 May-14 July with 69% of births occurring 14-24 May. All but 2 cows identified as pregnant at capture were observed with a calf. Fecundity was 0.82 and 0.85 calves per cow in 2002 and 2003, respectively; twinning rate was 3 of 15 (20%) and 2 of 20 (10%) each year. Calf mortality (observations of calves with radio-collared cows) at 2 months post-partum was similar both years (26 and 27%); cause of death was unknown in all cases, but was assumed to include predation by black bears and incidental mortality (e.g., abandonment, drowning; Child 1998).

The annual yearling/adult mortality was 27 (6 of 22) and 12% (4 of 26) in 2002 and 2003. Annual mortality of all moose due to vehicle collisions was 6% (all calves but 1) both years and occurred mostly (66%) in spring-summer. Hunting accounted for 4% mortality each year (all adult cows).

Radio-collared calves represented 56% (14 of 25) of overall mortality. Of 14 radio-collared calves in 2002, 8 dropped collars and the remaining 6 animals died over winter (1 December-1 May). Overwinter mortality of collared calves in 2003 was 38% (8 of 21). Of those calves that died over winter, most (66 and 63% each year) died from natural causes attributed to the combined or cumulative symptoms of malnutrition and parasites (winter tick, *Dermacentor albipictus*, lung nematode, *Dictyocaulus viviparus*); 93% of this type of mortality occurred during a 4 week period, 27 March-27 April. Mortality was in proportion to the sex ratio of marked calves.

Habitat Use

The number of seasonal locations per cow ($n = 9$) ranged from 9-43; the number of locations was not correlated to home range size ($P = 0.12$). Annual home range ranged from 15.5 to 66.4 km^2. Seasonal home range ranged from 2.2 to 46.5 km^2 but were largely similar, with mean fall range (17.4 km^2) significantly larger than mean spring range (7.8 km^2; $P = 0.008$). Although not statistically different, mean winter (15.1 km^2) and summer (14.1 km^2) ranges were both nearly 2X larger than mean spring range. Core areas (70% MCP) were 46% smaller, on average, than seasonal ranges (95% MCP) and varied from 1.1 to 37.0 km^2; no seasonal differences were detected, although the trend in size was similar to that with seasonal home range (Table 1).

The percent overlap of seasonal home range and core areas ranged from 20 to 34 and 12 to 27% (Table 2). The mean area and percent overlap of seasonal home ranges and core areas was greatest in summer and fall (7.7 km^2 and 34%, 2.8 km^2 and 27%) and smallest in winter and spring (3.6 km^2 and 20%, 1.0 km^2 and 12%). The area of overlap of home range and core area in summer and fall was greater than in winter and spring ($P =$

Table 1. Mean size and range (km^2) of seasonal home ranges (95% MCP), core areas (70% MCP), and mean number of locations per home range of 9 radio collared adult cow moose observed with a calf in consecutive years in northern New Hampshire, 2002-2003. Standard error for 95% MCP= 2.0 and for 70% MCP = 1.3.

	95% MCP		70% MCP		Mean # of Loc./Home
Season	Mean	Range	Mean	Range	Range
Winter	15.1	4.9-29.3	6.7	1.2-16.5	36.4
Spring	7.8	2.2-17.7	3.9	1.1-10.1	16.1
Summer	14.1	5.1-39.5	5.9	2.8-19.5	35.4
Fall[1]	17.4	3.3-46.5	8.6	0.8-37.0	19.4

Note: MCP = Minimum Convex Polygon.

[1]Greater than spring (P = 0.008) for seasonal range (95%).

0.006 and 0.008). The proportion of overlap of home ranges (P = 0.016) and core areas (P = 0.019) showed similar patterns; percent summer and fall overlap was greater than that in winter and spring.

The composition of habitat within annual and seasonal home ranges (Fig. 2) and core areas was similar. Deciduous (northern hardwood) forest was the dominant habitat in home ranges and core areas across seasons, comprising the largest percentage of home ranges and core areas in spring (38 and 37%). Coniferous forest was the second most abundant habitat type in all seasonal home ranges and core areas; availability of coniferous habitat was largest in summer (24 and 28%). Availability of mixed forest habitat was highest in fall home ranges (19%). Clearcut/regeneration stands were most prevalent in home ranges and core areas during fall (16 and 15%). Available wetland habitat within home ranges was lowest during spring (6%) and similar in other seasons. Core areas contained a higher proportion of available

Table 2. Mean size (km^2) and proportion of range overlap between consecutive seasons for seasonal home ranges (95% MCP) and core areas (70% MCP) of 9 radio collared adult cow moose observed with a calf in successive years in northern New Hampshire, 2002-2003. Standard error for overlap size = 0.8 for 95 and 70% MCP, for overlap proportion = 0.03 for 95 and 0.04 for 70% MCPs.

	Overlap Size		Overlap proportion	
Season	95% MCP	70% MCP	95% MCP	70% MCP
Winter-fall	6.7	1.4	0.28	0.15
Winter-spring	3.6	1	0.2	0.12
Spring-summer	4.8	0.9	0.29	0.12
Summer-fall	7.7[1]	2.7[2]	0.34[3]	0.27[4]
Winter-summer	5.7	1.8	0.27	0.22
Spring-fall	4.4	1.3	0.26	0.15

Note: MCP = Minimum Convex Polygon.

[1]Different from winter-spring (P = 0.006).

[2]Different from winter-spring (P = 0.008).

[3]Different from winter-spring (P = 0.016).

[4]Different from winter-spring (P = 0.019).

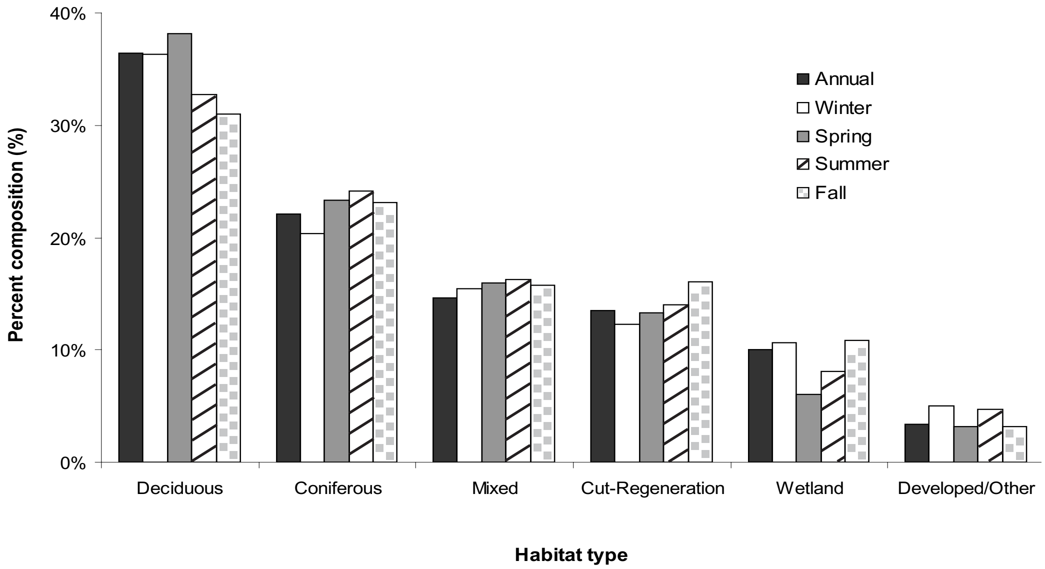

Fig. 2. Mean percent composition of annual and seasonal habitat types within home ranges of 10 reproductive adult cow moose in northern New Hampshire, 2002.

wetland habitat in winter (16%).

DISCUSSION

The daily capture rates in 2001 and 2002, without the use of a spotter plane and in variable snow conditions, were similar to those reported by Carpenter and Innes (6-10; 1995). Our capture rates were higher in 2003 (7-17) because snow (> 70 cm) impeded moose movement, increased sightability of moose, and provided optimal contrast for both pilot and net-gunner to recognize the optimal capture situation. Further, the spotter plane effectively reduced the search time of the helicopter crew, thereby increasing their effort in the actual capture process. Early winter, as suggested by Carpenter and Innes (1995), was an optimal time to capture moose in northern New Hampshire, and efficiency was improved with adequate snow cover and a spotter plane.

The capture mortality rate (4%, all calves) was between that reported by Carpenter and Innes (< 1%, 1995) and Olterman et al. (7%, 1994). Calves were apparently more susceptible to injury and mortality, as also suggested by data of Carpenter and Innes (1995). When net guns were not used, moose were immobilized chemically from the helicopter with no injury or mortality. The high capture rate and efficiency, and overall low mortality rate measured in this study point to the advantage of capturing moose from helicopters when large numbers of animals are desired.

The presumed accuracy of pregnancy testing in December (2 months post-breeding) was 90-95% with radio immunoassays and ultrasound (Stephenson et al. 1995, Huang et al. 2000). The pregnancy rates measured at capture in 2001 and 2002 (63% and 100%), and the proportion of marked cows observed with calves in spring (68% and 100%) were nearly identical, supporting the validity of our fecundity measurements derived from direct observations while stalking moose. The annual pregnancy estimates (68 and 77%) were lower than those of adult cows reported in populations below carrying capacity in Newfoundland (87%, Pimlott 1959), New Brunswick (79%, Boer 1987), Alaska (84-100%, Schwartz 1998), and Ontario (97%, Bergerud and Snider 1988). The observed twinning rates (10-20%) were analogous to populations considered near or above carrying capacity (1-25%; Edwards and Ritcey 1958, Blood 1974, Albright and Keith 1987).

As expected, calf survival (74 and 73%) through summer (2 months post-partum) was much higher than in areas with several large predators. Neonatal survival was only 17-27% in regions with bears and wolves in Alaska (Testa et al. 2000, Bertram and Vivion 2002). Substantial neonatal mortality (> 25%) was documented in this study in the first month when calves are most susceptible. However, calves radio-collared in December also experienced higher than expected over-winter mortality in 2002 (> 43% of calves died; 6 of 14 calves died, the rest dropped collars) and in 2003 (38%) presumably a result of malnutrition and parasites in March-April.

The annual survival rate of calves and yearling/adult cows and fecundity of yearling/adult cows measured in this study were used to calculate the predicted rate of population change with the Leslie-Lewis matrix method (Goodman 1980). This analysis, although premature with 2 years data, was conducted to assess the impact of the perceived high annual mortality of calves. Input data were 34% annual calf survival, 79% adult cow survival, and fecundity of 0.41 (female calves per yearling/adult cow). The annual finite rate of population change was 0.93, a value suggesting slight decline in the annual population associated mostly with calf mortality. The current (2001-2003) estimated population density in the study area is of 0.7 moose/km^2 (K. Bontaites, New Hampshire Fish and Game Department, unpublished data), has not changed since 1995, and is not the highest in the state (Adams et al. 1997).

Calf mortality was associated with the combined effects of malnutrition and high parasite loads. Although a high parasitic load is often described as a density-dependent characteristic, and tick-related mortality appears to be related to nutrition and overall body condition of the host, mortality is most pronounced when tick numbers are highest (Lankester and Samuel 1998). Presumably, calves are more susceptible than adult cows to the deleterious effect of ticks, particularly at high tick loads that produce excessive hair loss and anemia (Glines and Samuel 1989). However, tick abundance is not necessarily associated with moose density because environmental conditions are most important in determining tick density. Snow cover and cold temperatures reduce tick transmission rates to moose in fall and survival of engorged females in spring (Drew and Samuel 1989, Samuel and Welch 1991). Moderate snowfall within the project area may have contributed to increased tick density and subsequent tick loading on calf moose.

If malnutrition and mortality of calves in March-April was related to habitat quality, analysis of use and availability of seasonal habitats should indicate differential use. However, winter home range was not restricted in size relative to other seasons or compared to previous studies in New Hampshire and Maine (Table 1), and composition of available habitat was largely similar in all seasons (Fig. 2), implying that moose habitat was universally distributed across the study area. Further, moderate snow depth in both winters suggests that environmental conditions did not limit mobility or access to forage. Habitat in northern New Hampshire is generally considered high quality, with a mosaic of different age class stands distributed throughout the study area providing ample forage and cover as a result of commercial timber harvesting.

Consideration of the habitat use data in concert with population dynamics data suggests that both density dependent and independent factors could be influencing the study population. Pregnancy rates and fecundity rates were moderate, suggesting density dependent influence, yet habitat use and availability appear unconstrained. Summer home range sizes were smaller than

Table 3. Comparison of seasonal home range size estimates (km^2) of adult cow moose from selected studies using radio telemetry. Partially reconstructed from Hundertmark (1998).

		Season				
Location	Method	Winter	Spring	Summer	Fall	Reference
New Hampshire	MCP	15.1	7.8	14.1	17.4	This study
New Hampshire	HM	3.9	-	55.3	81.7	Miller (1989)
Maine	MCP	4.3	-	24.8	2.6	Thompson et al. (1995)
Minnesota[1]	HRF	3.6	-	12.7	-	Phillips et al. (1973)
Alberta	MCP	47	21.6	27	15.9	Lynch and Morgantini (1984)
Colorado	MCP	5	7.3	5.8	10.2	Kufeld and Bowden (1996)
Montana[2]	MCP	21.2	-	16	-	Van Dyke et al. (1995)
Alaska	MCP	43.1	-	39.8	60.6	Ballard et al. (1991)
Sweden	HM	4.9	6.9	9.1	5.6	Cederlund and Okarma (1988)

Note: MCP = Minimum Convex Polygon, HM = Harmonic mean, HRF = Home range fill.

[1]Summer range estimate consists of summer and fall locations.

[2]Winter range estimate consists of winter-spring locations and summer range consists of summer-fall locations.

reported in other studies in this region (Table 3). Adult cow mortality was low, yet calf mortality with minimal predation was high, and the calculated annual rate of change predicts population decline. Further, most calf mortality was associated with a parasite that does not necessarily reflect host density. Arguably, these collective data point to the complexity of habitat and population relationships, and the need to conduct long-term population studies. We presume that collection of similar data for two additional years will better clarify the factors most influential on the population dynamics of moose in northern New Hampshire.

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