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ASSESSING RELATIONSHIPS OF MOOSE POPULATIONS, WINTER TICKS, AND FOREST REGENERATION IN NORTHERN NEW HAMPSHIRE

By

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B.A., University of New Hampshire 2006

Thesis

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ABSTRACT

ASSESSING RELATIONSHIPS OF MOOSE POPULATIONS, WINTER TICKS, AND FOREST REGENERATION IN NORTHERN NEW HAMPSHIRE

By

Daniel H. Bergeron

University of New Hampshire, May 2011

This study examined relationships among winter ticks, weather, and the nutritional and reproductive status of moose, and the impact of moose on regeneration of commercial forests in northern New Hampshire. Three methods were evaluated to assess their usefulness as indices of relative winter tick abundance, and predictors of tick epizootics: tick counts on harvested moose and roadside, spring hair-loss surveys were considered time and cost effective to index winter tick abundance. Physical characteristics of harvested moose (1988-2009) indicated ovulation rates (~20%), and mean body weight (<200 kg) of yearlings declined since 1988; because adult body weight and ovulation rates remained stable, habitat quality was unlikely related. Winter tick epizootics are likely influenced by abnormal large scale weather events, as evident in the widespread die-off in 2002 associated with warm snowless conditions into mid-December 2001 that extended tick transmission to moose. Spring and fall weather should be monitored for unusual conditions causing high tick abundance and tick loads, particularly warm and snowless conditions in April and December. Mean stocking rate of all age classes of commercial tree species was above the threshold in all regions (49-87%); forest regeneration was not considered a regional problem at any moose density.

INTRODUCTION

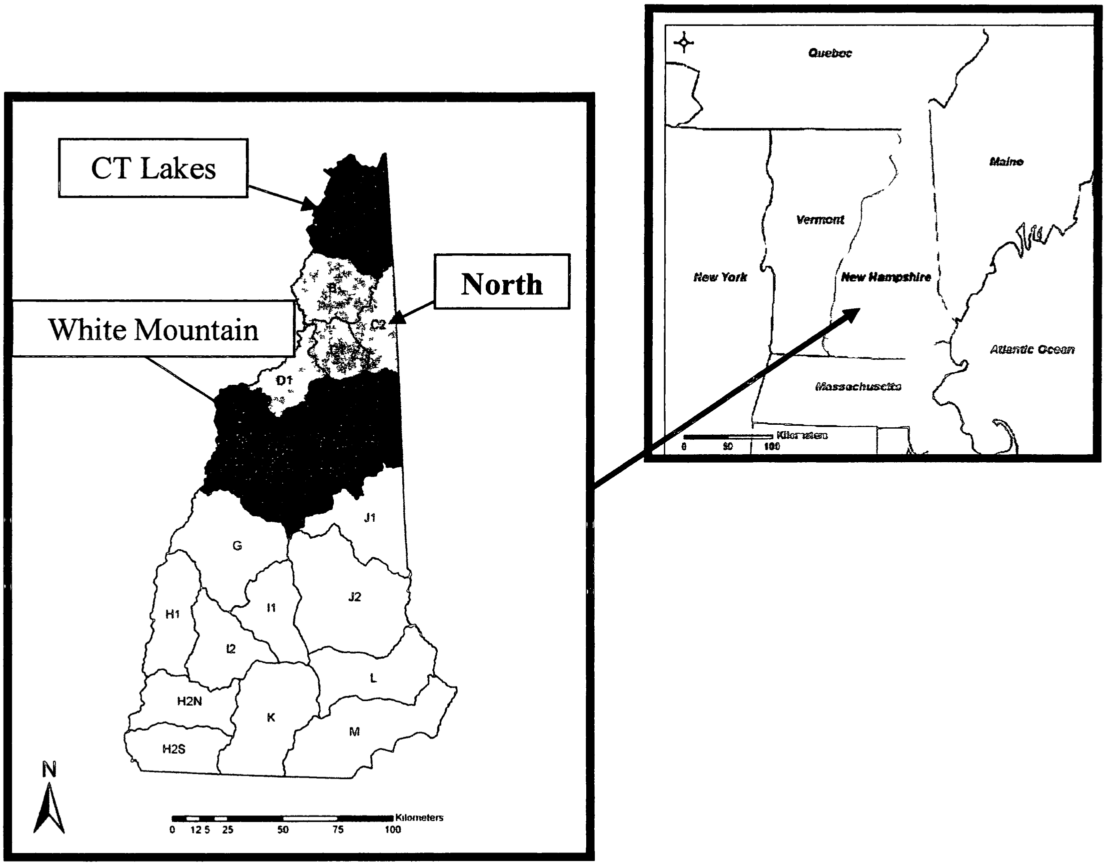
Winter ticks (*Dermacentor albipictus*) have been associated with large moose (*Alces alces*) die-offs (Delgiudice et al. 1997, Samuel 2004) and are suspected to influence population dynamics of moose in northern New Hampshire (Musante et al. 2010). Most recently, measurable calf mortality was associated with high winter tick infestation in 2002 (Scarpitti et al. 2005, Musante et al. 2010). Winter ticks are capable of having a dramatic impact on moose populations largely because they are a one-host parasite. They attach to moose as larvae in fall, develop all life stages throughout winter-early spring, and adult females drop to lay eggs in spring (Samuel and Barker 1979). The infestation of ticks on moose can be moderate-severe; the average number of ticks on a single moose in Alberta was ~32,000, with a maximum of >149,000 (Samuel and Welch 1991). Severe tick loads can lead to anemia (blood loss), restlessness, increased time spent grooming, less time spent feeding, hair-loss, and hypothermia (Samuel and Welch 1991, Addison et al. 1998b, Samuel 2004).

It is believed that the distribution of winter ticks is related to spring habitat use by moose because engorged adult female ticks and eggs are practically immobile (Samuel 2004). Moose in New Hampshire preferentially use cut/regeneration habitat in spring and early winter (Scarpitti et al. 2005), and such habitat use should directly influence the distribution and abundance of winter ticks across the landscape. Further, there is a direct relationship between quality and abundance of optimal moose habitat and commercial forest management (Scarpitti et al. 2005), and winter tick abundance is believed related to moose population density (Samuel 2004). However, high density moose populations can negatively impact hardwood and softwood regeneration; for example, Bergerud and Manuel (1968) found that repeated browsing of buds and branches can kill or suppress growth of hardwood saplings, and Brandner et al. (1990) found that damage to balsam fir (*Abies balsamea*) was greatest at high moose density. Therefore, potential relationships exist among moose productivity, habitat use, forest regeneration, silviculture, and abundance of winter ticks. Because moose can negatively impact forest regeneration, and both moose and forest management companies are important economic and social resources in northern New Hampshire, a challenging management situation often results relative to their balance.

STUDY AREA

The study area was located in northern New Hampshire in Coos, Grafton, and Carroll Counties and included New Hampshire Fish and Game Department (NHFG) Wildlife Management Units (WMU) A1, A2, B, C1, C2, D1, D2, E1, E2, E3, and F (Fig. 1). The study area was separated into 3 regions relative to difference in moose population density. The 3 regions from highest to lowest density were CT Lakes, North, and White Mountain; these regions were established based on the estimated indices of population density in the 2007 NHFG Annual Wildlife Harvest Summary. The CT Lakes region included WMU A1 and A2, the North Region WMU B, C1, C2, and D1, and the White Mountain region WMU D2, E1, E2, E3, and F. All study regions are ecologically, commercially, and recreationally significant to the state of New Hampshire. Possible predators of moose within the study area were black bear (*Ursus americana*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*), and white-tailed deer (*Odocoileus virginianus*) are sympatric with moose throughout.

The CT Lakes and North regions were dominated by hardwood species including sugar (*Acer saccharum*) and red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Red spruce (*Picea rubens*)-balsam fir tends to be the dominant forest type at higher elevations (>760 m) and in wet lowland sites (Degraaf et al. 1992). These regions are predominately forested and the majority of the land is privately owned and commercially harvested (Degraaf et al. 1992); they contain numerous wetlands, ponds, and lakes and are interspersed with trails and logging roads. The CT Lakes region is hilly with few



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high mountains, while the North is characterized by high mountainous terrain; elevation in the study was ~120-1900 m (400-6000 ft). Average moose density between 1995 and 2009 was 1.3 moose/km^2 (range = 0.83-1.59) in the CT Lakes region and 0.72 (range = 0.55-0.85) in the North region (Rines, moose project leader NHFG, pers. comm.).

The White Mountain region had the highest elevations and contained the White Mountain National Forest covering 304,050 ha that is ~97% forest (Costello 1995). It is dominated by beech, sugar maple, and yellow birch. Other common species include white ash (*Fraxinus americana*), red maple, red spruce, and eastern hemlock (*Tsuga canadensis*). Timber management practices are on a smaller scale than the other regions, with maximum clear-cut size of 10-12 ha (Costello 1995). The average moose density between 1995 and 2009 was 0.35 moose/km^2 (range = 0.15-0.28) (Rines, moose project leader NHFG, pers. comm.).

CHAPTER 1

INDEXING WINTER TICK ABUNDANCE

Introduction

The winter tick is a unique blood-feeding ectoparasite that is the only such species that has a dramatic impact on moose populations (Welch et al. 1991, Lankester and Samuel 1997). It is found in most of moose range in the United States and Canada south of 60° N latitude (Brown and Kohls 1950, Samuel and Barker 1979, Lankester and Samuel 1997), but not in Newfoundland or Alaska although could presumably survive if translocated (Zarnke et al. 1990, Lankester and Samuel 1997, Samuel 2004). In New Hampshire winter ticks have been collected as far south as Durham, Nottingham, Wilton, and Roxbury, but are more common in the northern part of the state (Eaton 2001), presumably due to the higher density of moose.

Winter ticks have 3 different parasitic life stages: larva, nymph, and adult (Samuel 2004). Each requires a blood meal to subsequently develop to the next stage, and meals are taken from the host throughout the course of one winter (Lankester and Samuel 1997, Samuel 2004). The life cycle of the winter tick is predictable with little annual variation (Addison and McLaughlin 1988, Addison et al. 1998a, Samuel 2004) because its reproductive cycle is dictated by fairly constant environmental cues such as temperature and photoperiod (Drew and Samuel 1986). Annual synchrony of the reproductive cycle is partly due to nymphal and adult diapause (Drew and Samuel 1986, Addison and McLaughlin 1988). Nymphal diapause allows larvae that attach to hosts at different times to be fully developed at the same time (Addison and McLaughlin 1988); adult diapause allows for synchrony of oviposition (Drew and Samuel 1986). This strict cycle is probably due to the northern climate that allows only a narrow window of reproductive success (Samuel 2004).

Eggs hatch into larvae in August-September after which they enter diapause (Wright 1969, Samuel 2004); the exact mechanism that activates ticks is unknown, but may be initial frost, photoperiod, or change in soil temperature (Samuel 2004). Larvae ascend vegetation to quest (wait to attach to a host) in September-October, and continue to quest until they find a host or until low temperature, wind, or snow causes them to become inactive and eventually die (Drew and Samuel 1985, Samuel 2004). Larvae feed from their host in October-November and begin to molt into nymphs. Nymphs stay on the host October-March, then feed and molt into adults in January-March. Adult ticks remain on their host from February-May, feeding and mating until they begin to drop off in March-April. The adult female then lays eggs in the leaf litter and dies (Samuel 2004, Samuel 2007); each is capable of laying thousands of eggs. The length of the parasitic phase may vary by location and host but is most influenced by latitude (Addison and McLaughlin 1988), suggesting that winter tick cycles are adapted to climatic differences in moose range. Weather appears to be the most influential factor of winter tick abundance (DelGuidice et al. 1997, Samuel 2004).

Moose density seems to influence the distribution and abundance of winter ticks as several studies indicated that tick load increases with moose density (Blyth 1995, Pybus 1999, Samuel 2004, 2007). It is believed that a higher density of moose allows for higher larval attachment in autumn yielding more adult females that produce more eggs (Samuel 2004); evidence for this relationship is mostly correlative.

Most larvae climb vegetation in the immediate area of the hatching site and 87% of engorged adult females are found within 60 cm of moose carcasses (Drew and Samuel 1985, 1986), indicating that the drop site of adult female ticks is essentially the site of oviposition. Therefore, distribution of winter ticks is related directly to where adult female ticks drop from moose during early spring (Drew and Samuel 1986, Samuel 2004). Moose in northern New Hampshire preferentially use cut/regeneration habitat in late winter-spring (Scarpitti et al. 2005), indicating the strong relationship between forest harvesting and the distribution and abundance of both moose and winter ticks.

Moose are the most severely affected host of winter ticks (Welch et al. 1991, Lankester and Samuel 1997, Samuel 2004) because they are poorly adapted to counteract infestations behaviorally (Anderson and Lankester 1974, Welch et al. 1991, Samuel 2004). Samuel (2004) estimated that the average tick load on moose is 28, 32, and 184 times higher than on elk, deer, and bison, respectively. Moose seem to be less effective groomers than other hosts due to inherent difference in grooming strategy (Welch et al. 1991, Mooring and Samuel 1998, Samuel et al. 2000). Elk, bison, and deer are programmed groomers (Mooring and Samuel 1998), or they groom in anticipation of, or before ticks have a chance to engorge and molt. Moose are stimulus groomers, that groom in response to the itch associated with feeding ticks (Mooring and Samuel 1998, 1999, Samuel 2004). Irritation from feeding ticks occurs when tick saliva causes a host cell to release histamine (Willadsen 1980, Mooring and Samuel 1998); therefore, grooming peaks in concert with engorgement by adult females (Mooring and Samuel 1998). Importantly, moose begin to groom after contracting their maximum tick load.

Moose may not be as effective in grooming against winter ticks because of a relatively short evolutionary relationship (Mooring and Samuel 1998, 1999, Samuel et al. 2000, Samuel 2004). Moose are relatively new arrivals to North America (Bubenik 1997, Mooring and Samuel 1999), and deer were probably the common host of winter ticks beforehand (Anderson and Lankester 1974, Holmes 1996, Samuel et al. 2000). Parasites are more likely to be pathogenic when exposed to "clean" hosts without adaptive mechanisms (Holmes 1996), thereby explaining why winter ticks minimally affect deer (Lankester and Samuel 1997) and have larger impact on moose (Mooring and Samuel 1998, 1999, Samuel et al. 2000, Samuel 2004).

Winter ticks are well adapted to be an effective parasite of moose. When larvae become active and quest they form clumps at the tips of vegetation ranging from a few to ~1,000 ticks (Drew and Samuel 1985, McPherson et al. 2000, Samuel et al. 2000), and are at the average chest height (~1 m) of moose, deer, and elk (Drew and Samuel 1985, McPherson et al. 2000). Peak larval activity coincides with the moose breeding season when moose are most active and the probability of attachment increases (Samuel et al. 2000, Samuel 2004). Bull moose are more active during the rut than females (Bubenik 1997), which may explain why bulls average twice as many ticks as females (Drew and Samuel 1985). Although bulls travel more during the rut (Bubenik 1997) and have a higher absolute number of ticks, calves are impacted more because they have proportionally more ticks per body size, are in poorer body condition than adults, and tend to be in severe negative energy balance in spring when impacts are greatest (Samuel 2004, Musante et al. 2007).

The average number of winter ticks on a single moose is ~30,000 and may exceed 100,000 (Samuel and Welch 1991, Samuel 2004). High tick loads can lead to several problems including damage and loss of the winter coat, less feeding due to increased grooming, reduced visceral fat stores, anemia, restlessness, reduced growth in young moose, and death (Samuel and Welch 1991, Samuel et al. 2000, Samuel 2004). Tick induced hair-loss or alopecia is one of the most common and visual impacts of winter ticks, and rapid hair-loss occurs in March-May, coinciding with increased engorging by adult ticks (McLaughlin and Addison 1986, Mooring and Samuel 1999). Increased hair-loss in March-May corresponds with increased grooming (Samuel 1991), and grooming and the amount of hair loss are positively correlated, with a lag in hair-loss of approximately one month (Mooring and Samuel 1999).

There are several negative impacts that are related to damage and loss of the winter coat including increased thermoregulatory costs and possibly hypothermia (McLaughlin and Addison 1986, Glines and Samuel 1989, Samuel 1991). Mooring and Samuel (1999) suggested that escalated heat loss due to loss of winter hair could lead to reduced visceral fat stores. Berg (1975) observed high calf mortality in northwestern Minnesota when calves died after 2 days of -30° C temperatures and winds of 130 km/h; all dead calves had severe tick infestations and hair-loss. However, hypothermia is likely not a mortal issue for wild moose because severe hair-loss rarely occurs before March, and prolonged severe cold is rare afterward (Welch et al. 1990). However, because moose are in a protein and energy deficit at the end of winter (Schwartz et al. 1988), increased energy and metabolic demands due to loss of hair may contribute to mortality associated with predation, disease (McLaughlin and Addison 1986), or hypothermia (Samuel 1991), especially in severe cold.

Experimentally infested moose with extensive hair-loss had lower average weight gain and fat stores than moose not infested with winter ticks (McLaughlin and Addison 1986, Glines and Samuel 1989, Addison et al. 1994). Weight may be affected by the negative correlation between time grooming and time spent feeding (DelGuidice et al. 1997, Mooring and Samuel 1999). Reduced feeding due to excess grooming is probably more important energetically than thermoregulatory costs for pregnant cows and undernourished moose in late winter (Samuel and Welch 1991). Reduced forage intake may also be due to an anorectic effect winter ticks have on their hosts (Mooring and Samuel 1999); however, there is no evidence that this occurs between moose and winter ticks as in cattle infested with *B. microplus* (cattle-tick) (O'Kelly et al. 1971, Seebeck et al. 1971). Moose stay bedded to conserve energy during periods of extreme cold (Renecker et al. 1978, Schwartz and Renecker 1997), however, moose can become restless from the discomfort associated with thousands of biting ticks (Samuel 1991, 2004), and this change in behavior may limit the energetic advantage associated with bedding and inactivity in late winter.

Anemia is likely the most severe problem caused by a high winter tick load. Glines and Samuel (1989) found that moose infested experimentally with winter ticks exhibited lower albumen and phosphate levels and anemia. Although Addison et al. (1998b) found few effects on the blood characteristics of captive moose, they cautioned that wild moose generally have higher tick loads and limited access to lower quality forage. Samuel (2004) calculated conservative estimates of the volume of blood loss to winter ticks (engorging adult females only) and estimated that bulls could lose a minimum of 5.4 L and need to replace 17% of their blood volume in March and April when adult females are engorging; cow moose would lose 3.2 L and need to replace 11% of their blood volume. Calves were impacted the most, losing about 8.1 L of blood and replacing 58% of their blood volume; these estimates indicate why winter tick-related die-offs are associated with calf mortality (Samuel 2004).

Musante et al. (2007) modeled the impact of different levels of tick infestations and concluded that blood loss associated with moderate-severe infestations of winter ticks would have measurable and substantial impact on energy and protein balance, and cause anemia and mortality of moose calves. They predicted that calves with moderate infestations could lose 1-2 times their blood volume during the peak engorgement period; >40% loss of blood volume over a short period of time can cause death (McGuill and Rowan 1989). Severely infested calves cannot sustain the energetic demands of blood regeneration primarily due to protein imbalance exacerbated by poor body condition and forage nutrition of low quality at the end of winter; calves are in a negative energy balance at the end of winter, will spend increased time grooming, and the peak engorgement period occurs prior to spring green-up. Conversely, winter ticks have less impact on larger adult moose in better relative nutritional state. However, blood loss and/or anemia might affect condition of pregnant cows and post-rut bulls, and although most adult moose probably survive tick infestation, productivity might decline.

The first recognition of the impact of winter ticks on moose populations was in 1869 (Samuel 2004), and multiple, large-scale moose die-offs have been attributed to winter ticks (Samuel 2004, Samuel 2007); the most recent in New Hampshire occurred in 2002 when most mortality of radio-marked moose was related to a winter tick epizootic (Samuel 2004, Scarpitti et al. 2005, Musante et al. 2010). In New Hampshire winter ticks probably have more influence on the moose population than predation, habitat, or human-related mortality factors, and predicting the frequency of tick epizootics is an important management consideration.

Flagging is a common technique used to estimate the yearly abundance of winter ticks and involves collecting ticks by dragging a sheet over vegetation during the questing period (Piesman et al. 1986, Ginsberg and Ewing 1989, Aalangdong 1994). It was used in Elk Island National Park to measure the relative abundance of winter ticks in different habitat types to assess whether moose distribution and density in spring dictate distribution and abundance of winter tick larvae (Aalangdong 1994). Digesting half hides of dead moose produces accurate measurement of tick load (Welch and Samuel 1989), but is impractical due to time and cost (Samuel 2007). Sine et al. (2009) developed a line transect method to count winter ticks on hide sections of harvested moose in Maine in an effort to estimate abundance and predict die-offs. This method appears to be more practical than hide digestion for field application, although it will likely require multiple years of measurements to develop a useful index.

The most common method of indexing winter tick abundance and impact on moose is by conducting hair-loss surveys in late winter (Welch et al. 1990, Samuel and Welch 1991, Wilton and Garner 1993). Hair-loss on moose is highly correlated with the rate of grooming against winter ticks (Mooring and Samuel 1999), and Samuel (2004) found that annual hair-loss correlated with the annual tick load of moose. Further, years with severe hair-loss coincide with large moose die-offs (Garner and Wilton 1993, Wilton and Garner 1993). Therefore, categorizing the annual level of hair-loss on moose should relate to the relative abundance of ticks on moose and presumably prediction of tick epizootics. Hair-loss surveys conducted since 1984 in Algonquin Provincial Park, Ontario have identified a range of hair-loss severity index values (HLI) that seem to coincide with moose die-offs (Steinberg 2008).

This study was designed to evaluate the accuracy and potential use of 3 approaches or methods to index winter tick abundance and epizootics: 1) flagging for larval winter ticks, 2) line-transect counts on harvested moose, and 3) hair-loss surveys.

Methods

Sampling for Larval Winter Ticks

In each region the relative abundance of larval winter ticks was measured during fall in 10-15 clear-cuts ≥4.05 ha (10 acres) and 2-5 years old. Each clear-cut was sampled every 7-14 days (5-7 times) from 21 September-12 December 2008 and

12 September-3 December 2009. Larval winter ticks were collected by dragging (flagging) a 1 m^2 white flannel sheet along parallel transects in each cut (Aalongdong 1994). The flannel sheet was attached to a dowel with 2 hose clamps, held to the side, and dragged over the top of vegetation. New transects were established each visit and separated by 10 m buffers to avoid repeat sampling. Transects were paced to measure length (m) for calculating tick density.

The date, time, sample site, and weather were recorded at the beginning of each sampling visit (Appendix A). Each flannel was inspected for tick larvae at the completion of a transect, and if positive with ticks, was stored in a clear plastic bag, labeled with the date, transect number, and clear-cut ID, frozen within 2 days, and counted at a later date (Aalongdong 1994). Sampling ended in each region when prolonged cold and/or permanent snow pack occurred; such conditions cause winter tick larvae to become inactive or die.

Ticks were counted by laying a flannel on a white background and recording with a tally counter (Aalongdong 1994). Each tick was removed from the sheet with masking tape to avoid double counts; this process was repeated on the opposite side of the sheet. The relative abundance of ticks per region (ticks/m^2) was calculated by tallying the total number of ticks in each region and dividing it by the total transect length sampled. Analysis of variance (ANOVA) was used to detect differences in relative abundance between regions and between sample years. Pairwise comparisons were made with Tukey's test; significance level was set *a priori* at 0.05 for all tests.

Winter Ticks on Harvested Moose

Winter ticks were counted on harvested moose brought to moose check stations run by NHFG. Counts were done for the first 5 days of the moose hunt (Saturday-Wednesday) in 2008-2010 at the primary check station in each of the sample regions: Pittsburg in the CT Lakes, Berlin Fish Hatchery in the North, and Twin Mountain Fish Hatchery in the White Mountain.

Winter ticks were counted in four 10 x 10 cm sampling plots on a moose carcass: 1) the neck at the base of the skull, 2) the upper edge of the shoulder blade, 3) the rump midway between the hipbone and the base of the tail, and 4) the edge of the rib cage (Fig. 1-1). Ticks were counted on four, 10 cm transects roughly 2 cm apart in each plot by combing back the fur and counting all ticks visible along each transect down to the exposed hide (Sine et al. 2009). Only moose that had been harvested within 5 h were sampled because ticks begin leaving a carcass a few hours after death. Time of death, moose seal number, and relative amount of ticks leaving the carcass were recorded at the beginning of each count (Appendix B). Moose biological data and sample region were later identified from the seal number.

A 10 x 10 cm hide sample was cut from each of the 4 transect locations, given hunter permission. Larger hide samples were removed and cut to size, then ticks were counted on the 4 transects on each sample as described above. Each hide sample was labeled with the date, seal number, location of the hide, and check station and then frozen in a sealed plastic bag. Total tick counts were conducted in a lab by digesting the hide samples; each was placed in a 1000 mL beaker with 800 mL of 5%

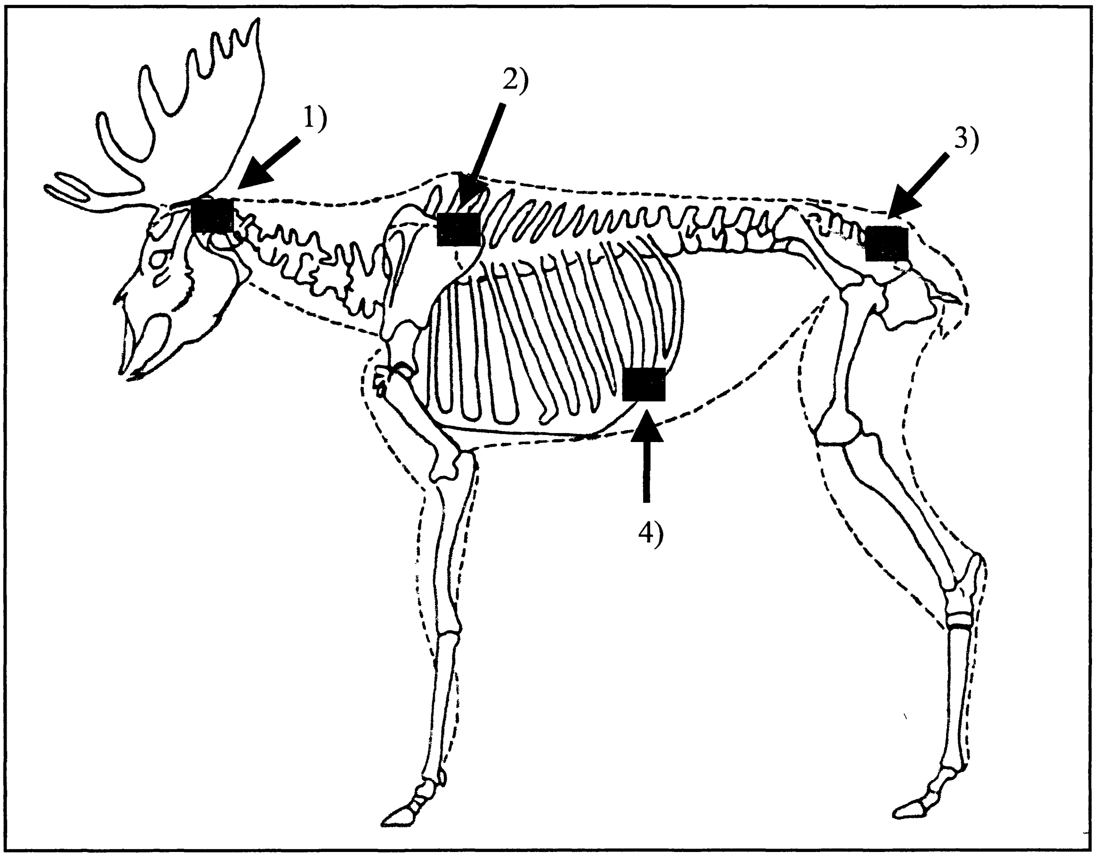

Figure 1-1. Location of 10 x 10 cm plots where ticks were counted and hide samples were removed from harvested moose in New Hampshire. The 4 locations were: 1) the neck at the base of the skull, 2) the upper edge of the shoulder blade, 3) the rump midway between the hipbone and the base of the tail, and 4) the edge of the rib cage (Sine et al. 2009).

potassium hydroxide solution heated to 90° C until it was fully digested (~2 h), leaving only the tick exoskeletons intact. The contents were filtered through a 180 µm sieve to separate undigested ticks that were counted under a lighted magnifier (Welch and Samuel 1989, Sine et al. 2009).

Linear regression analysis was used to examine whether the transect counts and hide digestion counts were correlated. This was done to assess the accuracy of performing only transect counts in the field. ANOVA was used to detect differences in transect counts between sample regions, year, and between bulls, cows, and calves. Pairwise comparisons were made with Tukey's test; significance level was set *a priori* at 0.05 for all tests.

Hair-Loss Surveys

Weekly hair-loss surveys were conducted from vehicles on predetermined routes in each of the 3 study regions to measure hair-loss on moose, 1 April-1 June 2009 and 19 April-25 May 2010. Routes were chosen to survey traditional roadside salt licks that moose were known to frequent in spring and early summer. Surveys coincided with when nymph and adult winter ticks take blood meals and hair-loss is highest (Samuel 2004). These surveys should be conducted as late as possible because grooming against ticks continues through April (Samuel 2007). The survey dates were adjusted in 2010 because few moose were observed at salt licks prior to 15 April in 2009. Two single-day surveys were also conducted in 2010 to compare with the larger survey.

Moose were assigned to 1 of 5 categories of hair-loss: no damage to hair, slight damage (~5-20% hair damaged/lost), moderate (~20-40%), severe (~40-80%), A regional calf:cow ratio was calculated from moose observed in each hair-loss survey. These were compared to ratios calculated the previous fall from moose hunter and deer hunter surveys conducted by NHFG. This exercise was done to investigate whether the proportion of calves declined from fall to spring; measureable calf loss associated with a winter tick epizootic would presumably be identified by a substantially lower calf:cow ratio in spring.

Results

Sampling for Larval Winter Ticks

In total, 17,036 ticks were collected on 11.7 ha of sample transect in 2008, and 11,759 ticks on 17.7 ha in 2009. The range of ticks per flagging sheet was 0-2,212. Although there was no difference among regions in the number of ticks either year or within regions between years, fewer ticks (~40-75%) were collected in each region in 2009. The average density in 2008 and 2009 was 0.19 and 0.11 ticks/m^2 in the CT Lakes (max = 1.30, 0.63), 0.16 and 0.07 in the North (max = 0.62, 0.40), and 0.08 and 0.02 in the White Mountain (max = 0.41, 0.10) (Fig. 1-2). There was a positive correlation between moose density and tick density both years ($r^2 = 0.93$ and 0.99).

Although no statistical differences were found among regions or between years, absolute differences were large. Mean number of ticks declined 42-75% within regions between years, and the mean number of ticks was 58 and 82% lower in White Mountain than CT Lakes in 2008 and 2009, respectively (Fig. 1-2). The mean number of winter ticks collected in individual clear-cuts was below the regional mean in the majority of cuts each year (50-92%), with the exception of White Mountain in 2008 (25%) (Fig. 1-3).

and worst case (>80%) (Appendix C). Moose were categorized by age and sex, and GPS locations, distinguishing characteristics, and pictures (not all moose) were used to help distinguish individual moose.

Repeat sightings were removed from the analysis by comparing obvious physical characteristics (e.g., antler growth) and pictures when available. Other potential repeat sightings were removed by analyzing GPS locations in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA). Buffers of 6.7 km^2 were placed around each moose location because this area represents the average spring home range of moose in New Hampshire (Scarpitti et al. 2005). If the buffers of 2 locations overlapped and the moose was categorized as the same age, sex, and hair-loss category, it was considered a repeat sighting and removed from the analysis.

An annual hair-loss severity index (HLI) was calculated for each of the 3 sample regions by assigning a number to each hair-loss category (1-5), multiplying the number of moose (M) in each category by that number, then dividing the sum of these numbers by the total (T) number of moose observed (Wilton and Garner 1993, Steinberg 2008):

$$\text{HLI} = \frac{(M \times 1) + (M \times 2) + (M \times 3) + (M \times 4) + (M \times 5)}{T} \qquad (1)$$

These values were compared to trends in flagging and check station data each year, and HLIs measured in Algonquin Provincial Park, Ontario. A HLI was calculated for bulls, cows, and calves with combined regional data both years to identify differences in HLI by sex/age.

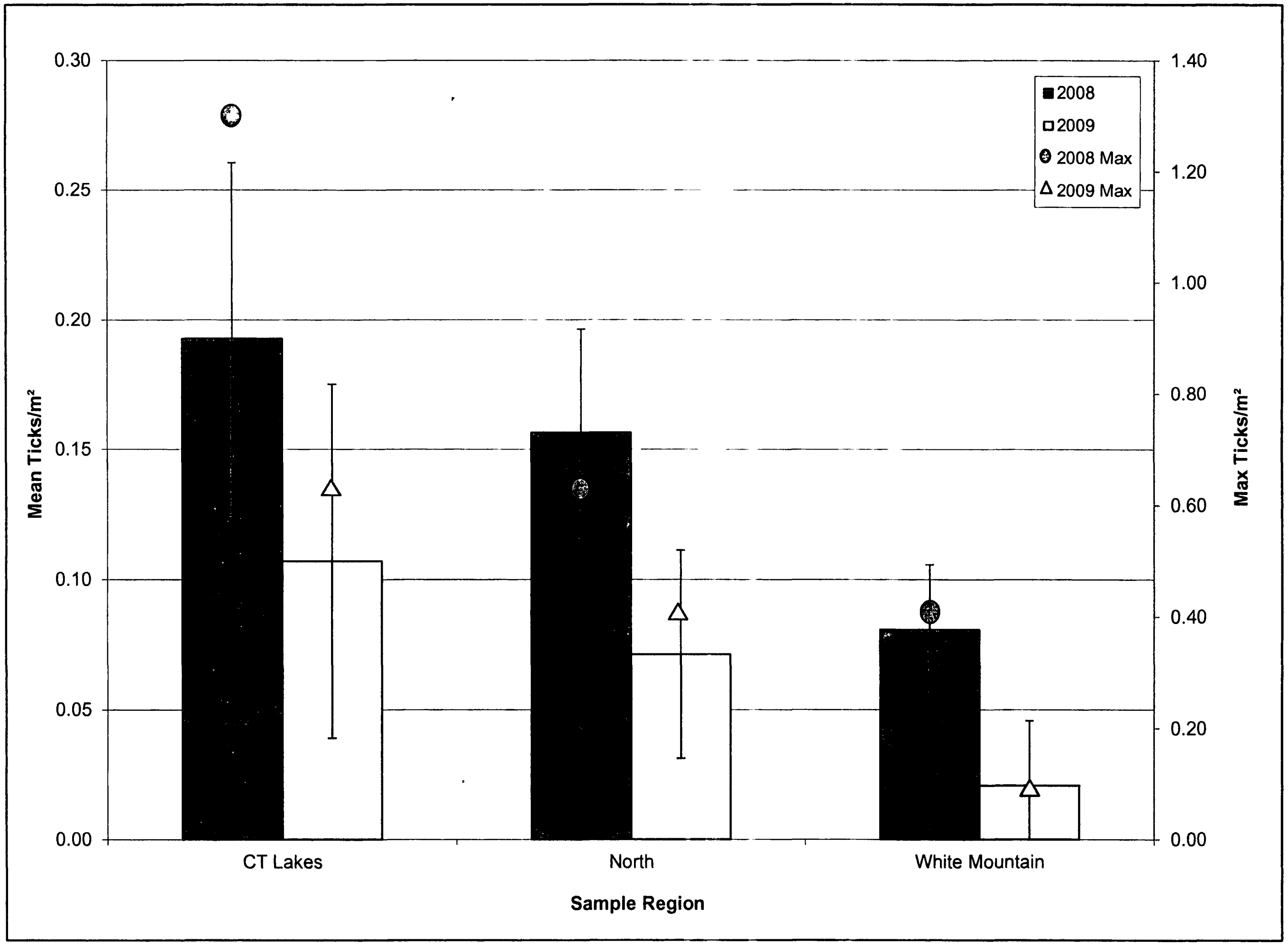

Figure 1-2. Mean (± SE) and maximum number of larval winter ticks collected while flagging clear-cuts in 3 sample regions of northern New Hampshire, 2008 and 2009.

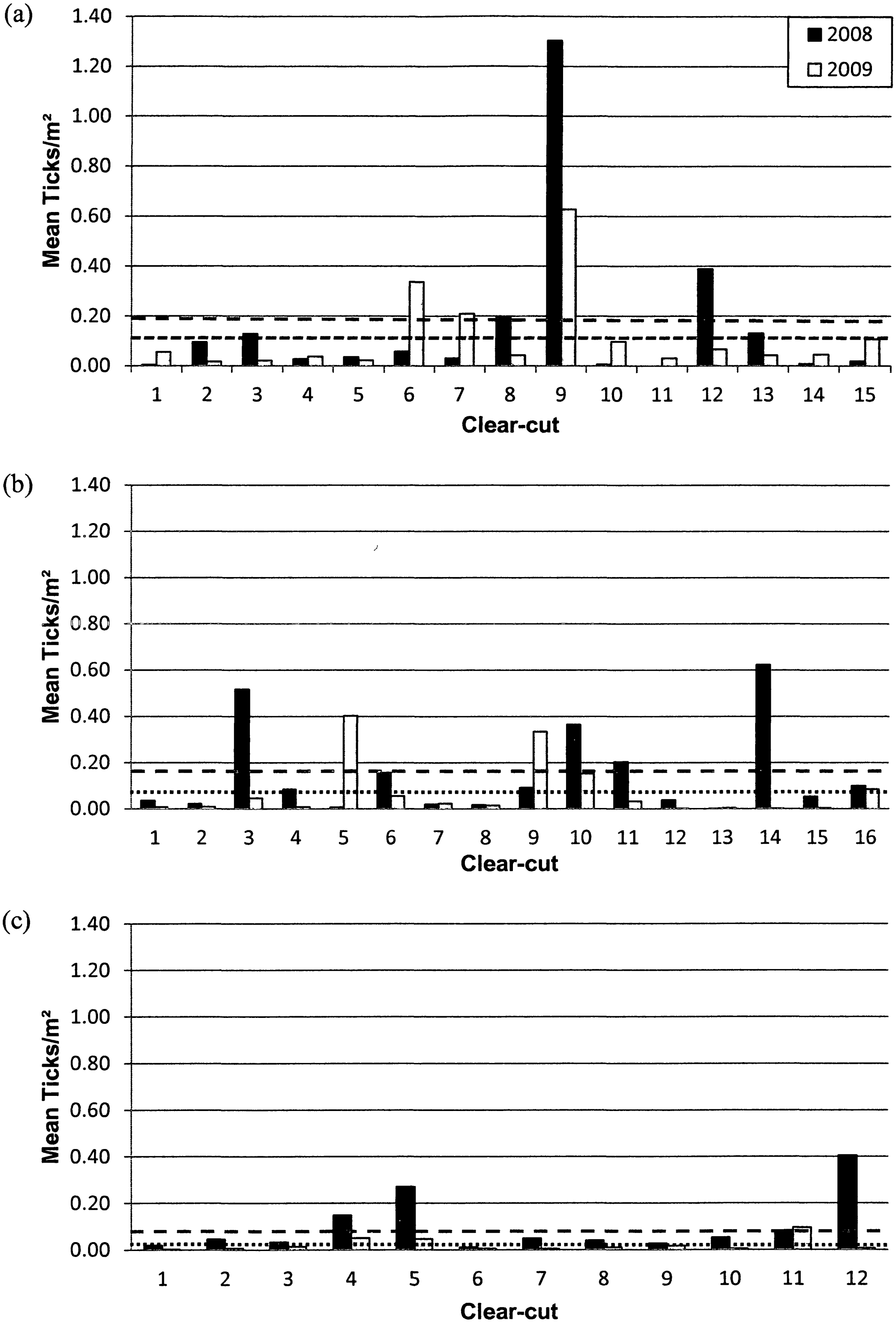

Figure 1-3. Mean number of larval winter ticks collected in individual clear-cuts in the CT Lakes (a), North (b), and White Mountain (c) regions, 2008 and 2009. The dashed and dotted lines represent the 2008 and 2009 regional means.

Winter Ticks on Harvested Moose

The mean number of ticks (all 4 areas and transects) counted on moose in the CT Lakes was 26, 25, and 51 in 2008, 2009, and 2010, respectively (Fig. 1-4). The mean number of ticks in the North was 73, 42, and 101 (Fig. 1-4). The mean number of ticks in the White Mountain was 14, 16, and 34 (Fig. 1-4). The mean number of ticks for combined regional data was 53, 31, and 79 (Fig. 1-4). Tick loads in the CT Lakes in 2010 were ~2X higher than in 2008 ($p = 0.034$) and 2009 ($p = 0.014$); tick loads in the North were ~1.8X higher in 2008 ($p = 0.034$) and ~2.4X in 2010 ($p = 0.000$) than 2009 (Fig. 1-4). The tick load in the White Mountain was not different from other regions or between years. Tick loads in the North were ~3X higher in 2008 ($p = 0.006$) and ~2X higher in 2010 ($p = 0.038$) than in the CT Lakes (Fig. 1-4). For all regions combined in 2010, tick loads were ~1.5X higher than 2008 ($p = 0.032$) and ~2.5X higher than 2009 ($p = 0.000$), and ~1.7X higher in 2008 than 2009 ($p = 0.024$, Fig. 1-4).

Because regional calf data were minimal, statistical analysis of bull:cow:calf relationships was for combined regional data. Calves had more ticks than adult moose each year and bulls had more than cows (Fig. 1-5). In 2008 tick load on calves was ~2X higher than bulls ($p = 0.014$) and ~6X higher than cows ($p = 0.000$) (Fig. 1-5). In 2009 tick load on calves was ~4.5X higher ($p = 0.004$) than on cows. In 2010 tick load on calves and bulls was similar and >2X that on cows ($p = 0.013$, Fig. 1-5).

A total of 148 hide samples were collected from 66 moose (26 bulls, 36 cows, 4 calves) in 2008 and 2009; 29, 45, 36, and 38 hide samples were collected from the neck, rib, rump, and shoulder, respectively. The number of ticks counted on transects

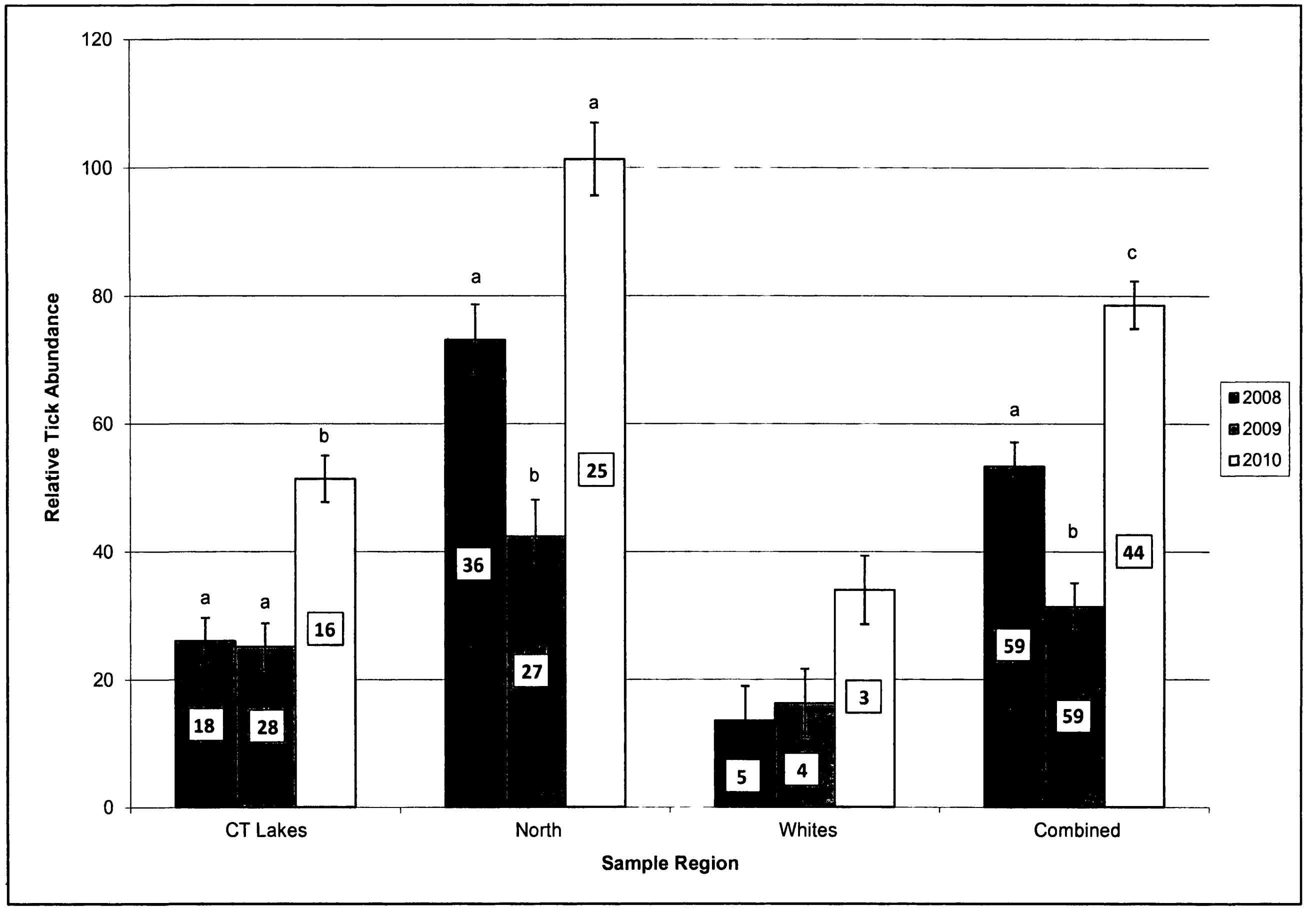

Figure 1-4. Mean (± SE) number of winter ticks counted on harvested moose in the CT Lakes, North, and White Mountain sample regions, and combined regional data, in northern New Hampshire, 2008-2010. Means are for all 4 areas of the hide and all transects combined. Numbers in columns represent sample sizes. Bars with unlike letters indicate significant differences within sample regions.

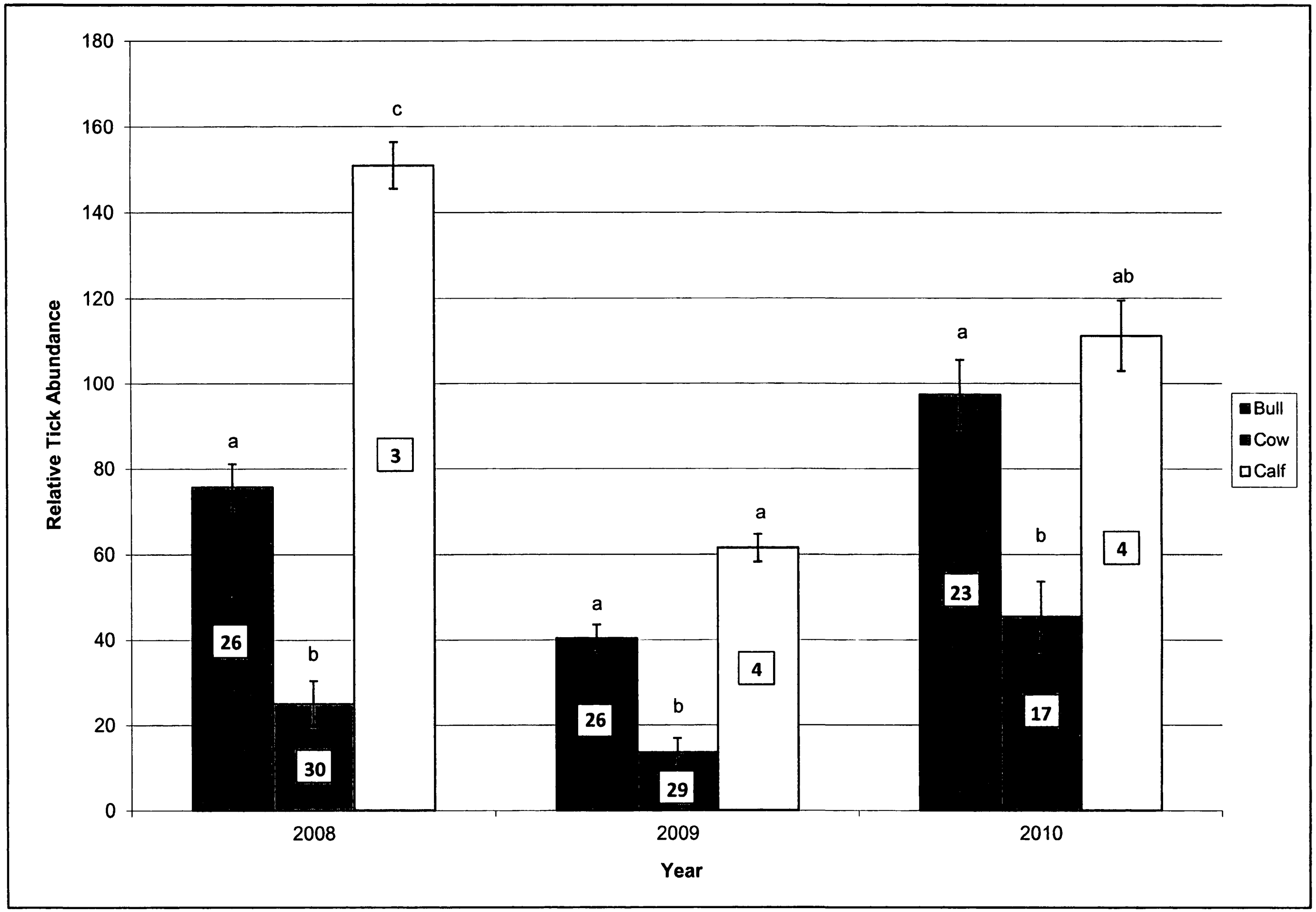

Figure 1-5. Mean (± SE) number of winter ticks counted on harvested bull, cow, and calf moose in northern New Hampshire; data are for all sample regions combined, 2008-2010. Means are for all 4 areas of the hide and all transects combined. Numbers in columns represent sample sizes. Bars with unlike letters indicate significant differences within sample year.

was positively correlated with the number of ticks after digestion for all areas of the hide; r^2 values ranged from 0.33-0.99. Counts on the rib had the weakest relationship ($r^2 = 0.33$-0.76), however, sample size was low ($n = 3$-9); combining regional and yearly rib samples yielded $r^2 = 0.70$. Combined regional and yearly data (Fig. 1-6) yielded similar r^2 values for each area of the hide and all areas combined ($r^2 \approx 0.80$).

Hair-Loss Surveys

A total of 256 and 222 moose were surveyed in the 3 sample regions during spring 2009 and 2010, respectively: 86 and 72 in CT Lakes, 96 and 77 in the North, and_74 and 73 in the White Mountain (Table 1-1). Moose in each category of hair-loss were observed each year. In 2009 the CT Lakes had the highest HLI (3.23), the North was 11% lower (2.91), and the White Mountain region was 2.35 or 24%_lower (Fig. 1-7). In 2010, HLI values were lower in every region (Fig. 1-7); the North region had the highest HLI (2.79), the CT Lakes was 14% lower (2.44), and the White Mountain region was 2.25 or 8% lower (Fig. 1-7).

Two single-day surveys were conducted on 12 and 24 May, 2010; however, only the North region produced enough sightings to make a single-day survey plausible. The most productive route ran from the Pontook Reservoir in Dummer, north along Route 16 to Errol (~17 miles). A total of 51 and 23 moose with corresponding HLIs of 2.67 and 2.17 were observed on 12 and 24 May (Table 1-1), values 4% and 29% lower than the regional survey. Only 8 and 3 moose were observed in the CT Lakes; the HLI was 2.00 both days (Table 1-1) and 22% lower than the regional survey. Only 9 and 8 moose were observed in the White Mountain region; the HLIs were 2.22 and 2.38 (Table 1-1), values similar to the regional

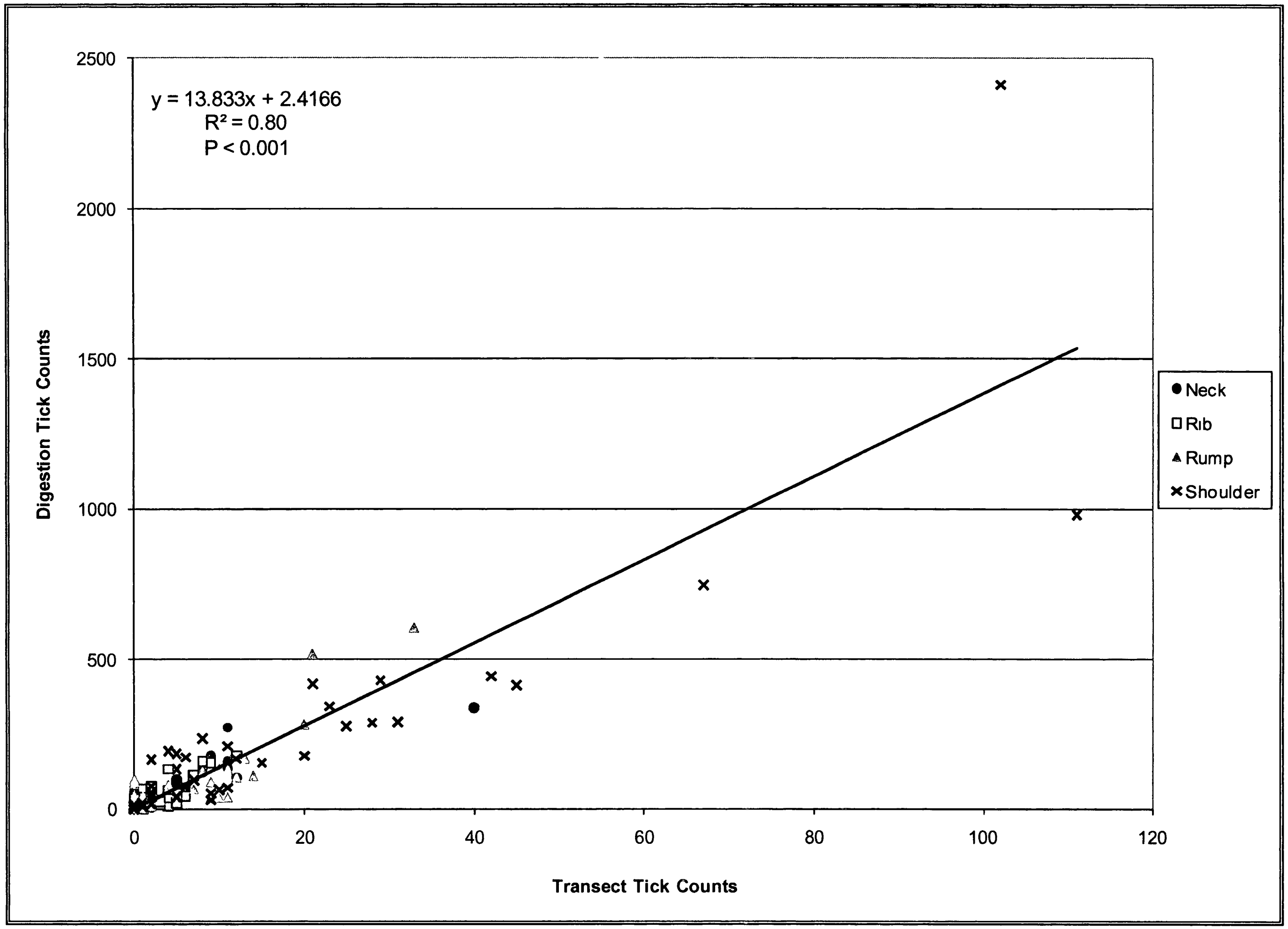

Figure 1-6. The relationship between the number of ticks counted on transects from 4 different areas on a harvested moose to the number of ticks counted after digestion of the corresponding 10 x 10 cm section of moose hide; combined data by area of hide, region, and sample years.

Table 1-1. Hair-loss severity index (HLI) values for 3 sample regions and bull, cow, and calf moose in northern, New Hampshire, 2009 and 2010. Single-day survey results for each region are included in parentheses (5/12/10 and 5/24/10). Bull, cow, and calf data were regionally combined by sample year.

Region/Moose	2009	n	2010	n
CT Lakes	3.23	86	2.44 (2.00, 2.00)	72 (8, 3)
North	2.91	96	2.79 (2.67, 2.17)	77 (51, 23)
White Mountain	2.35	74	2.25 (2.22, 2.38)	73 (9, 8)
Combined	2.86	256	2.50	222
Bull	3.07	90	2.65	83
Cow	2.70	111	2.45	103
Calf	2.75	36	2.29	35

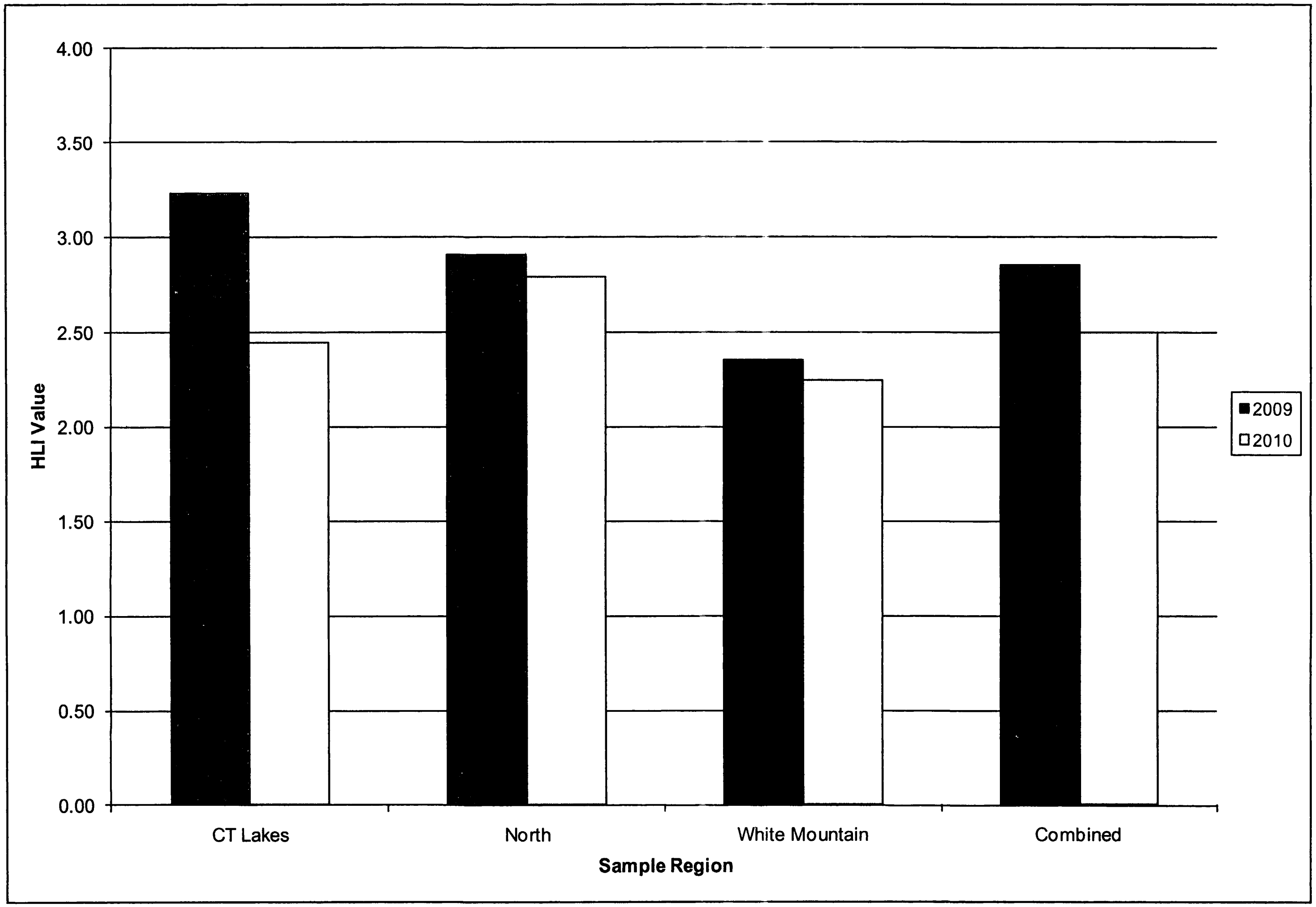

Figure 1-7. Hair-loss Severity Index (HLI) values for 3 sample regions in northern New Hampshire, 2009 and 2010.

survey. The HLI of bulls, cows, and calves ranged from 2.70-3.07 in 2009 and 2.29-2.65 in 2010, and varied little between sex/age of moose (2-16%); HLI of bulls was always highest (Table 1-1).

Calf:cow ratios calculated during spring hair-loss surveys were mid-range of the fall moose hunter and deer hunter surveys, except in the White Mountain region in 2010 when it was lower than both surveys (Table 1-2). There was little variation in calf:cow ratios among regions and between years; ratios ranged from 0.21-0.34 from moose hunter surveys, 0.33-0.41 from deer hunter surveys, and 0.30-0.43 from hair-loss surveys (Table 1-2). Variation was higher in calf:cow ratios from single-day surveys, which were lower than both moose and deer hunter surveys in the CT Lakes (0.14, 0.00) and White Mountain (0.20 both days) regions; however, the North region (0.38 both days) was mid-range of both moose and deer hunter surveys (Table 1-2). No evidence of a winter tick epizootic or major calf mortality existed either year.

Discussion

Sampling For Larval Winter Ticks

Larval tick abundance was correlated with regional moose density both years, which was consistent with trends identified in previous studies. In Elk Island National Park the average number of ticks on moose increased as moose numbers increased, with a 1-year lag (Samuel 2004, 2007); also, many documented large die-offs of moose in the park occurred at peak moose density. A die-off occurred in the Park in 1992, a year after tick density was 1.36 ticks/m^2 based on similar flagging measurements as employed in this study (conversions from Aalangdong 1994). This density is similar to the maximum values measured in New Hampshire clear-cuts, but

Table 1-2. Calf:Cow ratios calculated from moose harvest, moose hunter surveys, deer hunter surveys, and the corresponding spring hair-loss surveys in 3 sample regions of northern New Hampshire. Values for the 2010 single-day surveys (5/12/10, 5/24/10) in each region are shown in parentheses.

Year/Region	Harvest	Moose Hunter Survey	HLI	Deer Hunter Survey
2008/2009				
CT Lakes	0.14	0.26	0.30	0.33
North	0.22	0.21	0.34	0.38
Whites	0.21	0.32	0.33	0.36
2009/2010				
CT Lakes	0.14	0.25	0.34 (0.14, NA)	0.39
North	0.14	0.34	0.36 (0.38, 0.38)	0.44
Whites	0.18	0.34	0.31 (0.20, 0.20)	0.41

much higher than the regional averages (Fig. 1-2, 3). Moose density in the Park was ~2-4X higher than in New Hampshire suggesting a positive correlation between tick and moose density. Although it is intriguing to relate the high tick density in the Park with the epizootic, a similar density was measured in 1992 without a following die-off (although moose density was lower). Clearly relationships between abundance of winter ticks and die-offs are not exact, and direct comparison of estimates between disparate geographic regions is unwarranted.

The high variability in tick abundance in clear-cuts likely influenced the lack of statistical differences among regions and between years (Fig. 1-3). Regional means were highly influenced by a few cuts with high abundance of ticks, and the high variability among clear-cuts suggests that winter ticks are not evenly distributed within this preferred habitat type. Certain clear-cuts in each region had abundance 2-7X higher than the regional mean both years (Fig. 1-3); this distribution pattern may explain why individual hair-loss varies annually, and certain moose have severe hair-loss in years of overall light infestation. Local sites of high tick density may also relate to why epizootics occur across wide geographic ranges that encompass variable moose population densities.

A benefit of this sampling method is that it can extend through the entire questing period, which usually occurs from September until colder temperatures and snow kill remaining unattached larvae (usually November-December) (Drew and Samuel 1985, Samuel 2004); questing usually stops at <0° C (Samuel and Welch 1991). Because our sampling occurred from early-mid September through the first substantial snowfall, it should be representative of the relative abundance of ticks.

However, because temperature and snow condition varied considerably among the adjacent study regions, tick abundance alone would not necessarily reflect regional tick loads. However, it may be possible to detect annual regional trends in tick abundance because tick numbers declined in each region from 2008 to 2009 (Fig. 1-2). The data were also suggestive that moose density influences tick abundance because tick density was correlated with regional moose density both years.

The flagging technique is probably not practical to index tick abundance or tick loads because it is extremely labor intensive and costly. Sampling occurred for ~3 months and across a wide geographic range. Two people sampled a clear-cut in ~2 h and each needed to be visited multiple times; workdays averaged 8-10 h, with extensive driving along logging roads. Larvae also had to be counted at a later date and each flannel required 10 min->1 h depending on the number of ticks. The relative length of the questing period is probably most easily estimated by tracking ambient temperature and snow cover, and assuming that an extended warm fall will lengthen the questing period and tick load.

Winter Ticks on Harvested Moose

Tick loads were higher in the North region than the CT Lakes and White Mountain regions each year (Fig. 1-4); the White Mountain had low sample size each year. This differed from the flagging study (larval sampling) in which tick numbers were correlated with regional moose density. Fewer ticks were counted in 2008 than 2009, whereas numbers were higher in 2010 (Fig. 1-4). Interestingly, some adult winter ticks (some engorged) were observed on moose in 2010, which is unusual because the majority of ticks at this time of year are nymphs (Drew and Samuel 1989, Samuel 2004). This may indicate early questing that allowed ticks time to take blood meals and molt into subsequent life stages. These trends were in agreement with larval sampling results as both indicated a reduction in tick abundance from 2008 to 2009.

More ticks were counted on calves than bulls and cows each year (Fig. 1-5) which was consistent with previous studies (Welch and Samuel 1989, Sine et al. 2009). Bulls tend to have the highest absolute numbers of ticks due to their size and increased activity during the rut (Samuel 2004); however, calves have proportionally more ticks (per area) due to their smaller body size (Samuel and Barker 1979, Samuel 2004). In Maine, Sine et al. (2009) found twice as many ticks on calves than adults.

There was a strong relationship between transect counts and total counts from hide digestions. R^2 values were high (>0.60) for all areas of the hide with the exception of the rib in the North region both years; however, sample sizes were relatively low ($n = 3$-9). The strongest relationships occurred when data from all areas of the hide were combined ($r^2 = 0.80$, Fig. 1-6). Sine et al. (2009) found similar results ($r^2 = 0.88$) when combining hide samples and concluded that the total number of ticks counted on all transects was the best predictor of tick density on moose.

Due to the strong positive correlation between transect and total counts in both studies, hide samples were not collected in 2010; transect counts (easy and efficient) should suffice for use as an index of relative tick abundance on harvested moose. Average time to count the 4 areas of hide was ~5 min with a separate counter and recorder, and about twice as long if done alone (same as Sine et al. 2009). Further, some hunters were unwilling to donate hide samples and laboratory work was tedious and labor intensive; hide samples took ~2 h to digest and counting tick exoskeletons varied greatly from <1 h-2 days.

The transect method identified differences between regions and years, but did not indicate a positive correlation with moose density like the flagging method. Because the moose harvest in New Hampshire occurs in mid-October, this method may not translate directly to tick load and/or related moose mortality if moose disproportionately acquire ticks in late fall. Aggregations of winter tick larvae can survive into November (Samuel and Welch 1991), and tick larvae were collected into December during flagging. Tick numbers on harvested moose in October might also reflect an active early questing period as suggested by the presence of adult ticks in 2010. However, if the timing of the hunting season remains constant, a useful index of relative tick abundance could be developed with additional years (5-10) of data.

Hair-Loss Surveys

HLI values in 2008 were correlated positively with moose density, with the highest value in the CT Lakes region followed by the North and White Mountain regions (Fig. 1-7), similar to results from larval sampling. In 2009 values dropped in every region, and the North region had the highest HLI followed by CT Lakes and the White Mountain regions (Fig. 1-7), a trend similar to that found on harvested moose. All methods indicated a reduction in tick numbers from 2008 to 2009 with combined data from all regions (Figs. 1-2, 1-4, and 1-7). This suggests that singly, none of the methods is sensitive enough to detect potential differences in tick abundance among regions, but all are probably capable of detecting large annual shifts in relative tick abundance.

Hair-loss surveys conducted in Algonquin Provincial Park, Ontario since 1984 (Steinberg 2008) had HLI values ranging from 1.18-3.48; HLI's ≥2.50 were associated with mortality events. HLI values in this study were 2.20-3.23 with the majority >2.5 (Table 1-1), but no major mortality event was evident. However, documentation of moose mortalities is limited in New Hampshire making it difficult to identify die-offs in the state. The HLI values in New Hampshire should not be compared directly with those in Algonquin Park because helicopter surveys are usually conducted in March due to snow cover. Surveys in New Hampshire took place in April-May when more hair-loss should be evident because grooming continues through April (Samuel 2007).

Bulls had the highest HLI both years (Table 1-1) which was in agreement with studies suggesting that bulls carry the highest number of ticks due to their activity patterns during the fall questing season (Drew and Samuel 1985, Samuel 2004). However, there was little variation (2-16%) in the HLI of bulls, cows, and calves indicating that sex/age of moose should have little influence on survey results (Table 1-1). Hair-loss surveys were labor intensive and costly when conducted ~8 h daily for 2-3 days weekly in April-May. Further, the issue of identifying individual moose to avoid repeat sightings is somewhat problematic; use of distinguishing photographs was effective but difficult to acquire for all moose. Repeat sightings are not an issue during single-day surveys because the observer can distinguish individual moose and movement would be negligible. A minimum of 50 moose is considered an adequate sample in Algonquin Provincial Park (Steinberg 2008); however, only on 12 May in the North region (n = 51) was this level reached in a single day survey (Table 1-1).

The HLI (2.67) was similar (4% lower) to that of the weekly survey (2.79), suggesting that a single-day survey might suffice if an adequate sample size (~50) is realized. Single-day HLIs in the White Mountain region were also similar to weekly results (within 1-6%), but sample size was <10.

Surveys in New Hampshire should be conducted as multiple, morning surveys preferably condensed within a 5 day period (1 May-15 May) that are focused on the most commonly used roadside saltlicks in a region; a survey would be complete with ≥50 individual moose. Routes within a region should be separated to ensure that the same moose is not observed at different licks by multiple observers (or use a single observer). This would reduce the length of the surveys, distance traveled, and time spent removing repeat sightings. Surveys should also be conducted on cool mornings with little precipitation to enhance sightings. Removing the White Mountain region from sampling seems logical because it consistently yielded the lowest abundance of ticks regardless of method, and has the lowest density of moose.

Because calves are most highly impacted by winter ticks and are the cohort most susceptible to mortality, estimates of fall and spring calf:cow ratios should indicate substantial mortality events that reduce the proportion of calves in the population. Calf:cow ratios calculated from fall hunter surveys and spring hair-loss surveys were reasonably similar (Table 1-2), and calf:cow ratios during the single-day survey in the North region (n = 51) were similar to those in the weekly survey (Table 1-2). Low sample size may be problematic for calculating such ratios in spring, and the reliability and sensitivity to detect such change is unknown because no evident die-off occurred. However, HLI calf:cow ratios should be useful if an adequate sample size (n ≥50) is reached.

Although moose density and tick abundance were generally related in New Hampshire, weather plays a strong role in the abundance and distribution of winter ticks (Samuel 2004). Regional weather differences that impact ticks at different life stages likely influenced regional tick abundance regardless of moose density. Because major tick related die-offs are usually concurrent and widespread geographically (Samuel 2004), tracking regional differences in New Hampshire may not be as important as obtaining adequate tick load samples from harvested moose and at least one regional sample of 50 moose.

The combination of fall tick counts on harvested moose and spring hair-loss surveys should prove useful to index winter tick abundance in northern New Hampshire. They are both time and cost effective and capable of indicating annual change in relative tick abundance. Check station counts provide an indication of transmission during the questing period; however, if weather conditions were to extend the questing period into December check station counts may not be representative of actual tick loads. Hair-loss surveys should help identify high tick abundance in late winter-spring caused by an extended questing period. Calf:cow ratios obtained during hair-loss surveys could prove useful in detecting years of high calf mortality. Combined use and comparison of these methods will allow for more confidence in their index value, and of particular importance is identification of threshold values associated with major die-offs. Indices of tick abundance could be linked to die-offs if moose mortalities were more thoroughly documented in the state.

CHAPTER 2

TEMPORAL ASSESSMENT OF PHYSICAL CHARACTERISTCS AND REPRODUCTIVE STATUS OF MOOSE IN NEW HAMPSHIRE

Introduction

Physical characteristics are commonly used to estimate population health in different species. For example, age-specific body weight of male and female moose is directly related to health and production (Schwartz and Hundertmark 1993), and in yearlings onset of ovulation (Saether and Heim 1993). Antler measurements are used to estimate the health of deer populations because of the correlation between antler size and nutritional status (McCullough 1982); antler size in moose is influenced by many factors including nutritional status and health (Bubenik 1997a). Adams and Pekins (1995) concluded that yearling moose in New Hampshire were useful for estimating herd health due to the substantial weight gain, change in antler characteristics, and onset of ovulation in this age class; they found measurable differences in body weight and number of corpora lutea in yearling cows relative to other age classes.

Winter ticks appear to have greatest impact on moose population dynamics through direct mortality or lower nutritional condition of calves. Reduced growth in young moose surviving infestations seems probable, although few studies are conclusive. Glines and Samuel (1989) observed significant weight loss in an experimentally infested calf, and McLaughlin and Addison (1986) noted that 9 captive moose calves infested experimentally with ticks had lower average weight gains than uninfested moose. Berg (1975) suggested that high calf mortality could lead to a reduction in cohort size in succeeding years, and Musante et al. (2010) predicted that lower calf survival would reduce recruitment and lower fitness in yearlings would reduce growth and reproductive rates. Negative influences include lower twinning rates and productivity, declining corpora lutea counts and ovulation rates, and reduced body weight of yearling cows (Musante et al. 2010).

Age, antler spread, beam diameter, number of points, corpora lutea count, and body weight have been measured on hunter-harvested moose since 1988 in New Hampshire. Given the relationships between certain physical characteristics and nutritional status of a moose population, periodic analysis of these data should reveal trends and change in the relative condition of the moose population in New Hampshire. In this study I assessed temporal trends in physical characteristics and relative nutritional and reproductive status of moose in New Hampshire from 1988-2009.

Methods

Biological data collected from harvested moose at New Hampshire check stations in 1988-2009 were analyzed to assess whether temporal change has occurred in the physical condition of the moose population. Data were broken into 3 time periods (1988-1998, 1999-2004, and 2005-2009) and analyzed by sample region. Measurements included age and field-dressed body weight for both sexes, number of corpora lutea for female moose, and beam diameter, spread, and number of points for antlered moose.

Antler beam diameter was measured with a micrometer on one antler at 2 perpendicular sites 2.54 cm above the pedicle; the average diameter was recorded. Antler spread was the maximum distance measured between any 2 points, and an antler point was ≥2.54 cm long. Ovaries were collected and stored in denatured ethyl-alcohol then later sectioned to visually count the number of corpora lutea (Cheatum 1949). Age was determined by cementum annuli counts from a lower incisor (Sergeant and Pimlott 1959).

A subset of similar data was obtained from Maine and Vermont to compare with New Hampshire data. Maine data included only field-dressed body weight of cows and Vermont data were from 1993-2009 only.

New Hampshire data were analyzed initially by time period and sample region, and combined statewide for comparison with Maine and Vermont data. Analysis of variance (ANOVA) was used to test for age-specific differences in physical parameters; age classes were 0.5, 1.5, 2.5, 3.5, 4.5, 5.5, and ≥6.5 years. Pairwise comparisons were made with Tukey's test and significance level was set *a priori* to 0.05 for all tests.

Results

Females

The only differences within an age class between time periods in any region were in the yearling age class. Yearling body weight declined ~25 kg from 1988-1998 to 2005-2009 in the North (10%, p = 0.000) and White Mountain (15%, p =

0.003) regions, and from 1999-2004 to 2005-2009 in the CT Lakes region (5%, p = 0.033) (Fig. 2-1, Appendix E). Corpora lutea in yearlings declined from 1988-1998 to 2005-2009 in the North (68%, p = 0.000) and White Mountain (76%, p = 0.003) regions, and from 1988-1998 to 1999-2004 in the CT Lakes region (43%, p = 0.009) (Fig. 2-2, Appendix F); corpora lutea counts were ≤0.21 across all regions in 2005-2009. Ovulation rates of yearling cows declined 39, 49, and 56% in the CT Lakes, North, and White Mountain regions, respectively, from 1999-2004 to 2005-2009 (Appendix F). Mean body weight of cows with 0 corpora lutea was 199 kg in New Hampshire and 198 kg in Vermont.

Yearling body weight declined 6% in Vermont (11 kg, p = 0.001) from 1999-2004 to 2005-2009 (Fig. 2-1), but corpora lutea counts, although lower, were not different. Corpora lutea were lower in Vermont than New Hampshire in 1988-1998 (45%, p = 0.030) and 1999-2004 (38%, p = 0.030) (Fig. 2-2); there was no difference in 2005-2009, albeit all counts were historical lows. Yearling body weight in New Hampshire and Vermont was not different. Body weight of Maine yearlings increased 3% from 1988-1998 to 1999-2004 (p = 0.012) (Fig. 2-1). Body weight was 6% lower in Maine than New Hampshire in 1988-1998 (p = 0.000), but 7% higher in 2005-2009 (p = 0.000) (Appendix E). Body weight of Maine yearlings increased 9% from 1988-1998 to 2005-2009. The proportion of yearlings >200 kg in New Hampshire, Vermont, and Maine was 44, 32, and 62%, respectively, in 2005-2009.

Males

The only differences found between time periods in any sample region were in the yearling age class. All measurements except antler beam diameter declined in

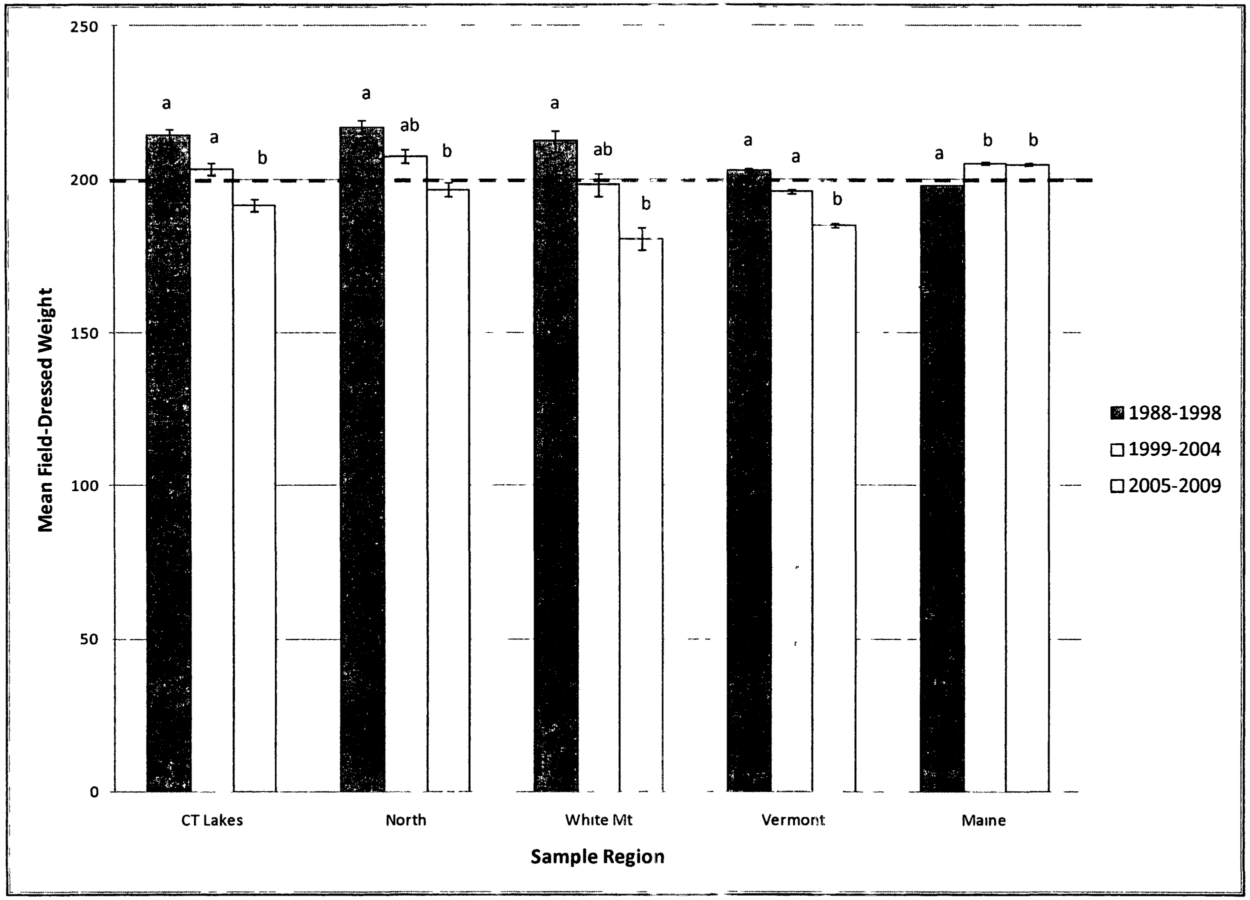

Figure 2-1. Mean (±SE) field-dressed body weight (kg) of harvested yearling cow moose in 3 sample regions of New Hampshire and statewide in Vermont and Maine, 1988-2009; Vermont data are from 1993-2009. Bars with unlike letters are significantly different within sample region and between time periods. The dashed line represents mean body weight of New Hampshire yearlings with 0 corpora lutea (199 kg).

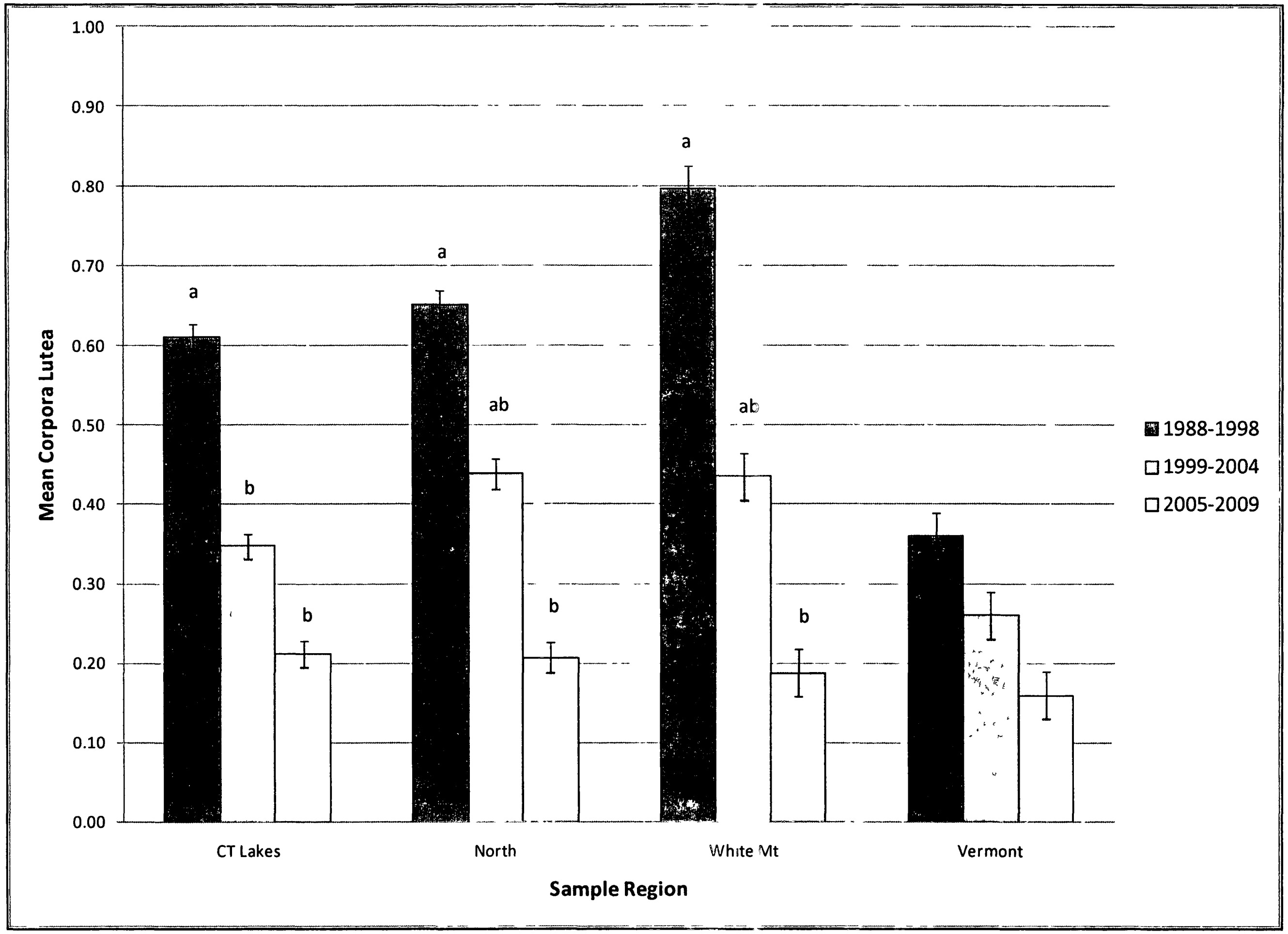

Figure 2-2. Mean (±SE) corpora lutea (CL) of harvested yearling cow moose in 3 sample regions of New Hampshire and statewide in Vermont and Maine, 1988-2009; Vermont data are from 1993-2009. Bars with unlike letters are significantly different within sample region and between time periods.

yearlings in the North region. Yearling body weight declined 23, 11, and 28 kg from 1988-1998 to 1999-2004 in the CT Lakes (10%, p = 0.000), North (5%, p = 0.011), and White Mountain (15%, p = 0.000) regions, respectively (Appendix G). Yearling antler points declined from 1988-1998 to 1999-2004 in the North (15%, p = 0.022) and White Mountain (33%, p = 0.016) regions, and from 1988-1998 to 2005-2009 in the CT Lakes region (33%, p = 0.021) (Appendix H). Yearling antler spread declined 12, 8, and 17% from 1988-1998 to 1999-2004 in the CT Lakes (p = 0.034), North (p = 0.026), and White Mountain (p = 0.001) regions, respectively (Appendix I). Yearling antler beam diameter declined 11% from 1988-1998 to 1999-2004 in the CT Lakes (p = 0.023) and White Mountain (p = 0.014) regions (Appendix J).

As in New Hampshire, Vermont yearlings declined in every physical characteristic except antler beam diameter; body weight declined 6% from 1988-1998 to 1999-2004 (p = 0.003) (Appendix G), antler points declined 20% from 1999-2004 to 2005-2009 (p = 0.037) (Appendix H), and antler spread declined 7% from 1999-2004 to 2005-2009 (p = 0.049) (Appendix I). There was no difference between body weight or antler points in New Hampshire and Vermont yearlings; antler spread was greater in New Hampshire than Vermont in 1988-1998 (9%, p = 0.031) and 2005-2009 (5%, p = 0.028), and antler beam diameter was 6% greater in Vermont than New Hampshire in 1999-2004 (p = 0.033).

Discussion

Prior research suggested that New Hampshire's moose population was stabilizing based upon an estimated growth rate that was negligible (0.95-1.07), due in large part to average body weight <200 kg and a corresponding 25% reduction in ovulation rate of yearling cows from 1988-1998 to 1999-2004 (Musante et al. 2010). A continued decline in body weight and corpora lutea count of yearling cows occurred in 2005-2009. Yearling ovulation rates in North America average 49% (range = 0-100%, Schwartz 1997), and the New Hampshire rate was less than half this in 2005-2009 (19-21%, Appendix F). Conversely, adult rates have remained normal (60-97%, Appendix F) (Schladweiler and Stevens 1973, Schwartz 1997); rates and trends in Vermont were similar (Appendix F).

Cows <200 kg are considered non-reproductive (Adams and Pekins 1995), and not coincidently, mean body weight of cows with 0 corpora lutea was 199 kg in New Hampshire (1988-2009) and 198 kg in Vermont (1993-2009) (Fig. 2-1, 2). Maine does not collect corpora lutea data, however, the peak mean yearling body weight was 205 kg (Fig. 2-1), only marginally above the reproductive level. Productivity from the yearling age class in New Hampshire and Vermont is expectedly low based on ovulation rates ≤20% that are considerably lower (1/3-1/2) than those prior to 2000. Mean corpora lutea count in New Hampshire (0.22) and Vermont (0.16) was equal to half the proportion of yearlings >200 kg (0.44 and 0.32, respectively). Assuming this relationship, the mean corpora lutea in Maine is probably ~0.30, as 62% of yearlings are >200 kg.

Several factors including habitat quality, weather, and disease/parasites, contribute to declining trends in physical parameters of a moose population. However, Musante et al. (2010) believed that moose in New Hampshire were mostly influenced by the annual impact and particularly epizootics of winter ticks. Mortality of their radio-collared moose was mostly due to winter kill/parasites (41%) associated with winter tick infestations; mortality due to hunting, road-kill, poaching, predation, and weather was not considered major during the 3 year study (Musante et al. 2010). Further, habitat was considered adequate because field-dressed weights, reproductive data, and survival of adults were not low or declining, or representative of a habitat-limited population. Similarly, this analysis identified no declining trends in adult physical characteristics or ovulation rates.

Calves are most severely impacted by winter tick infestations (Samuel 2004, 2007) and some mortality is likely an annual event (Musante et al. 2010); however, even surviving calves presumably experience lower body weight and reduced fecundity as yearlings (Samuel 2004, Musante et al. 2010). The declining trend in yearling condition in New Hampshire and Vermont from 1988-2009 seemingly indicates that average tick loads probably impact moose populations through annual calf mortality and reduced fecundity of yearlings. Although the field-dressed body weight of yearling cows in Maine has been stable at 205 kg since 1999, it is less than the peak weight realized in New Hampshire (217 kg, 1988-1998, Fig. 2-1). As a region, it is evident that productivity of yearling cows is low with corpora lutea counts probably <40% even in Maine based on comparative data from New Hampshire and Vermont (Fig. 2-1, 2).

New Hampshire's moose population was still expanding in 1988-1998, and physical characteristics may have peaked during this period of high resource availability and extensive forest harvesting in the 1980s (see Bontaites and Gustafson 1994). Subsequent decline in physical characteristics may reflect stabilization in the population after saturation of available habitat, and reduced forest harvest and forest regrowth. However, decline in yearling body weight and ovulation rate below the North American average suggests that other contributing factors exist, particularly given the stability of measurements in adult moose. In fact, calves have higher relative tick loads than adults, and severe hair-loss is evident on individuals even in low/average tick years.

The lack of a documented epizootic since 2002, yet continuing decline in yearling physical characteristics, suggests that annual winter tick infestation of calves have measurable influence on yearling growth and fecundity. Environmental conditions that enhance reproduction and questing of winter ticks will presumably maintain this relationship. The continued decline in yearling fecundity lends strong support for models that indicate population stability (or at least minimal growth) of the moose population in northern New Hampshire. Continued monitoring of winter tick loads, hair-loss, and physical parameters of harvested moose is warranted to best document and manage this moose population.

CHAPTER 3

RELATIONSHIP BETWEEN WEATHER AND WINTER TICKS

Introduction

Several factors influence the distribution and abundance of winter ticks, but weather appears to be the most influential factor on abundance (DelGiudice et al. 1997, Samuel 2004). Specifically, low temperature and snow cover in late winter-early spring negatively impact survival of adult winter ticks (Drew and Samuel 1985, 1986, Timmerman and Whitlaw 1992), temperature and precipitation influence survival of eggs in June-August (Aalangdong 1994, Samuel 2004), and survival of larvae is influenced by snow, temperature, and wind in October-November (Samuel 1989, Welch 1991). Drew and Samuel (1986) placed engorged adult female ticks in either leaf litter or snow and found only 11% survival on snow; mortality was presumed due to prolonged exposure at temperatures below the threshold for survival (-17° C). Cold dry summers result in lower egg production and survival (Samuel 2004); lower and upper critical temperatures for reproduction are 15 and 30° C (Glines 1983). Strong fall winds often blow larvae from vegetation while prolonged exposure to snow and cold kill larvae (Samuel 2004). Questing of larvae stops at <0° C or when larvae become covered by snow; inactivity at low temperatures in fall ends questing and the transmission period to moose (Samuel and Welch 1991).

The majority of moose die-offs associated with winter ticks have occurred when engorged adult females drop on leaf litter versus snow the previous spring

(Samuel 2007). Further, the severity of spring hair-loss and moose die-offs are directly related to the mean April temperature the prior year (Wilton and Garner 1993). Hair-loss and mortality of moose increased at spring temperatures >3-4° C suggesting that higher survival of engorged adult females results in more larvae and higher transmission in fall. It is believed that low spring and fall temperatures coupled with early winter snow limit the geographic spread of winter ticks to Alaska (Zarnke et al. 1990).

Temperature and snow cover in spring and fall have most influence on survival of winter ticks and their infestation of moose. Therefore, monitoring weather during these seasons when adult ticks drop from moose and larvae quest for hosts may help predict winter tick infestations associated with major moose die-offs. This study examined weather conditions in 2008-2010 when winter tick abundance, fall tick-load on moose, and spring hair-loss surveys of moose were monitored simultaneously. Weather conditions in 2001 were also examined for comparison because a winter tick epizootic and moose die-off that occurred in New Hampshire and surrounding states in spring 2002.

Methods

Regional weather measurements were obtained from the National Climatic Data Center: the First Connecticut Lake weather station (#27-999-01) in the CT Lakes, the Berlin weather station (#27-0690-01) in the North, and the North Conway weather station (#27-5995-02) in the White Mountain. Monthly and daily mean ambient temperature, precipitation, and snow fall were calculated in each region for

2001, 2008, 2009, and 2010; snow cover was not available for fall 2010. Mean regional temperature and precipitation were obtained for 1971-2000.

These data were compared to indices of tick abundance developed from fall larval sampling, check station counts, and spring hair-loss surveys to investigate relationships between seasonal weather and tick abundance. Data were compared between sample regions and years. Weather data were also compared to the corresponding data in 2001, the year preceding the 2002 moose die-off in New Hampshire, in an attempt to identify weather conditions that may predict/cause die-offs.

Results

CT Lakes

Mean April temperature was ≤4° C in 2001, 2008, and 2009, but nearly 6° C in 2010 (Fig. 3-1). Mean April snow depth was minimal in 2009 and 2010, but >35 cm in 2001 and 2008 (Fig. 3-2). Mean monthly temperature was between 15-30° C in summer (June-August) except June 2009 (Table 3-1), and precipitation was within the normal range for the region each year. Mean monthly temperature was >0° C during questing months (September-November) except November 2008 (Fig. 3-3); mean December temperature was <0° C each year and warmest in 2001 (-3.4° C, Fig. 3-3). The onset of permanent snow cover (>25 cm) came earliest in December 2009, 2001, and 2008, respectively; there was no snow cover until 15 December in 2001 (Fig. 3-4)

North

Mean April temperature was >6° C in all years except 2001 (4.0° C, Fig. 3-1). Mean snow depth in April was minimal in 2008-2010, with bare ground in 2009 (Fig.

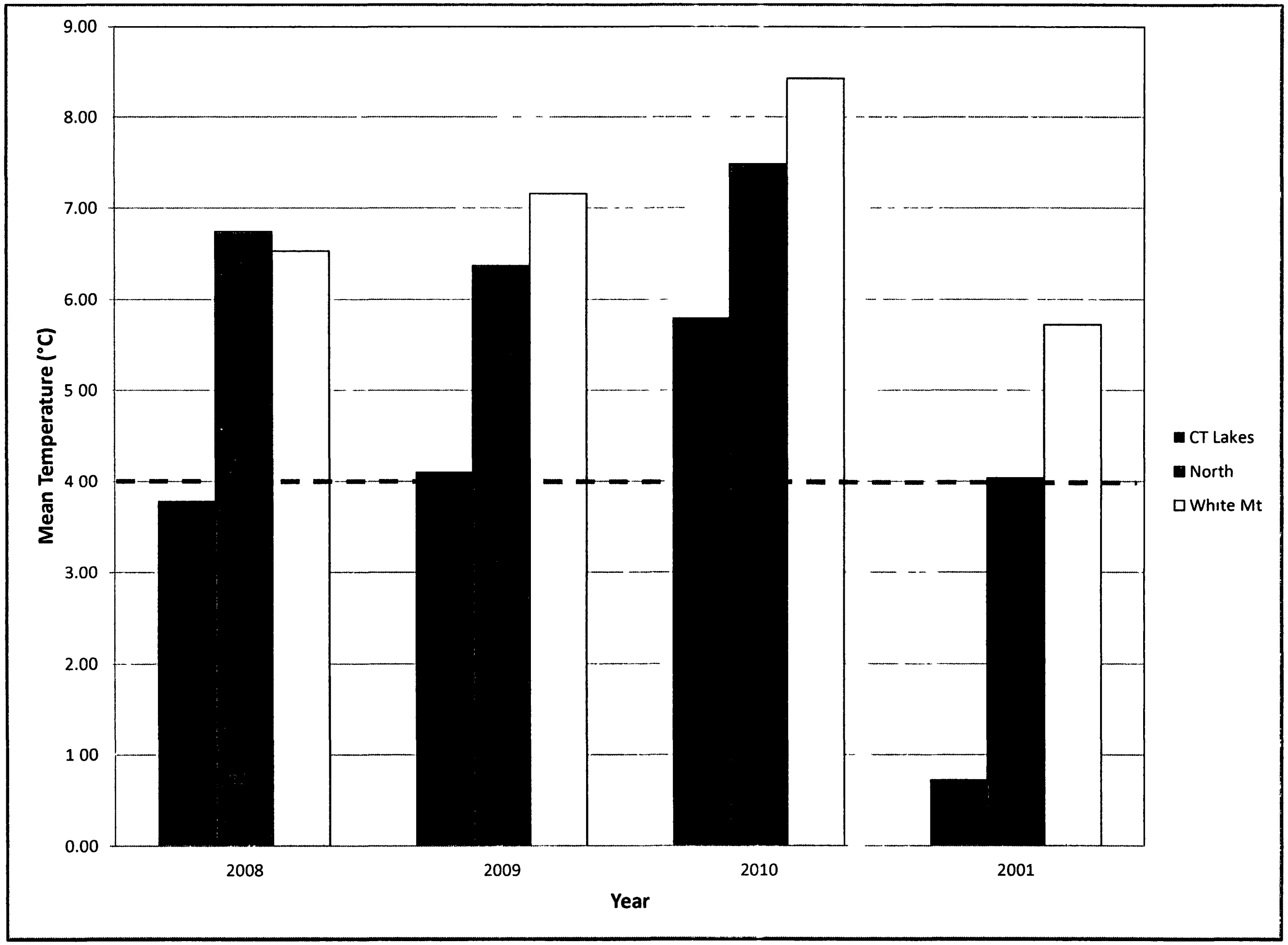

Figure 3-1. Mean April temperature in 3 regions of northern New Hampshire in 2001 and 2008-2010. The dashed line represents the temperature (4° C) at which winter tick survival begins to decline this time of year (Wilton and Garner 1993).

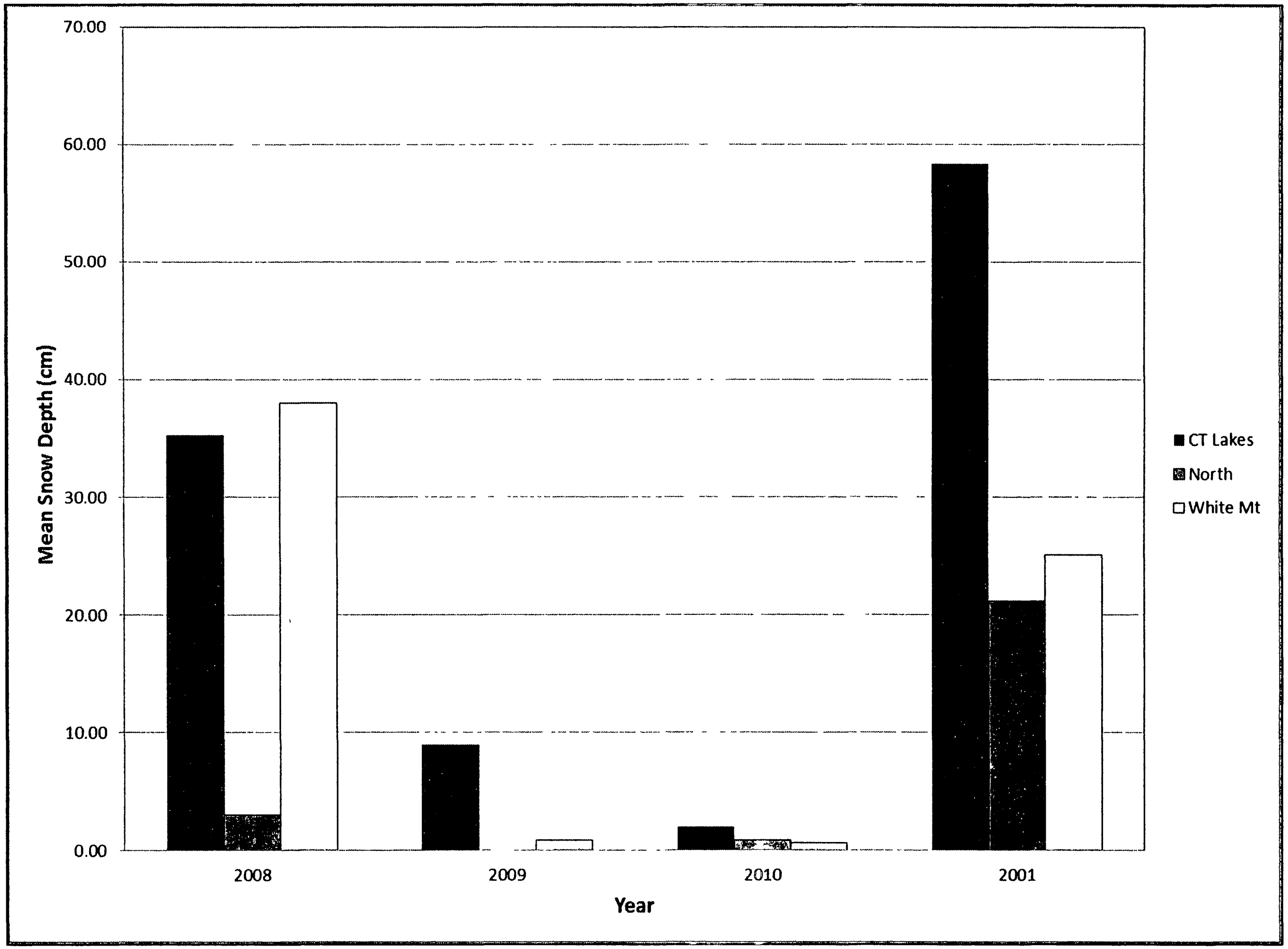

Figure 3-2. Mean April snow depth (cm) in 3 regions of northern New Hampshire, 2001 and 2008-2010.

Table 3-1. Average temperature (° C) during summer (June-August) in 3 regions of northern New Hampshire, 2001 and 2008-2010. The upper and lower thresholds for reproduction of winter ticks are 15 and 30° C (Glines 1983).

Region/Year	2001	2008	2009	2010
CT Lakes				
June	15	15	14	15
July	15	18	16	19
August	17	16	17	17
North				
June	18	17	15	16
July	18	20	17	21
August	20	17	19	18
White Mountain				
June	20	18	16	17
July	20	20	18	22
August	22	18	20	19

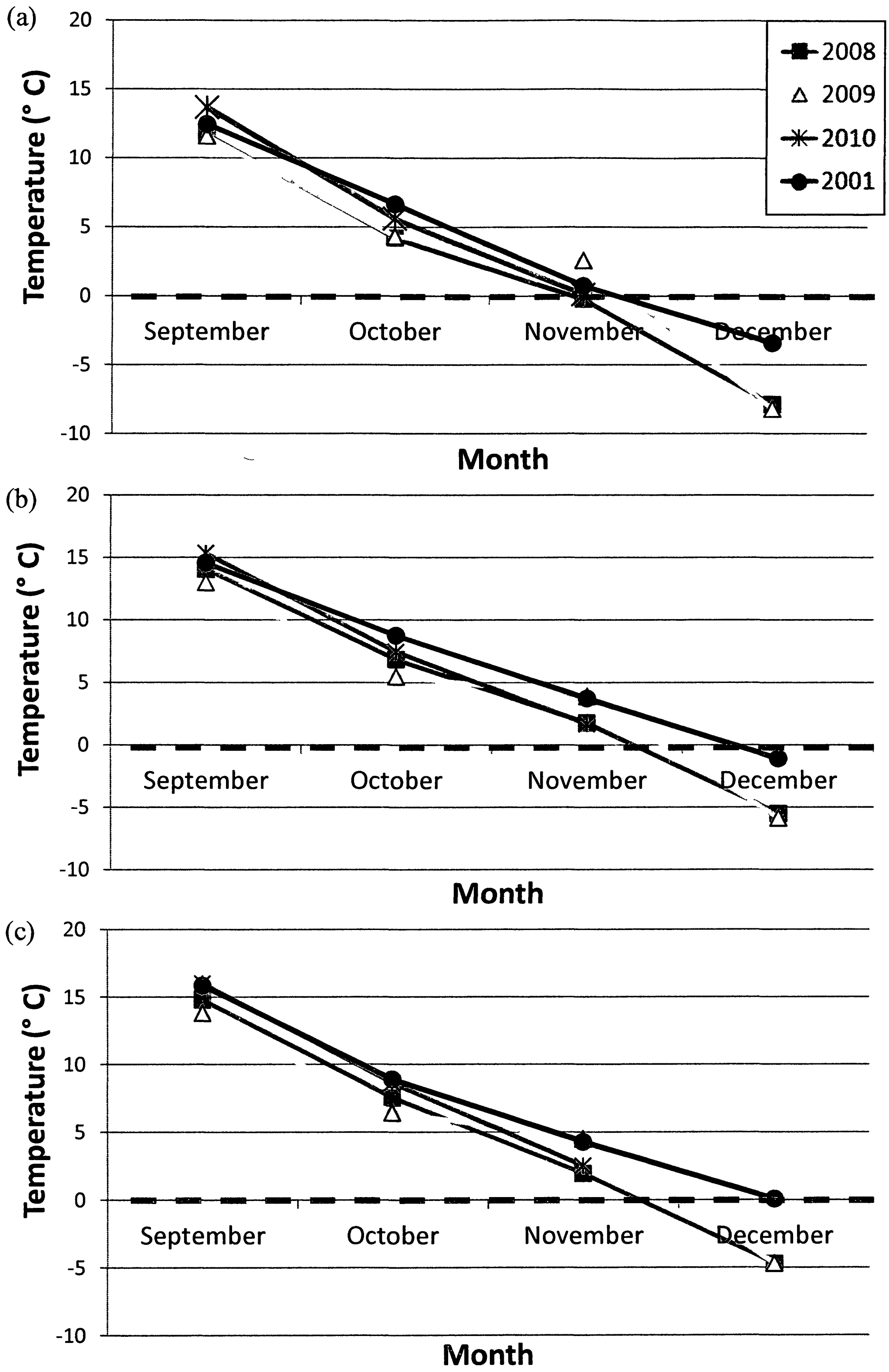

Figure 3-3. Mean monthly temperature (° C) during the questing period (September-December) of winter ticks in the CT Lakes (a), North (b), and White Mountain (c) regions, 2001 and 2008-2010. The dashed line represents the temperature (0° C) where questing declines/stops (Samuel and Welch 1991).

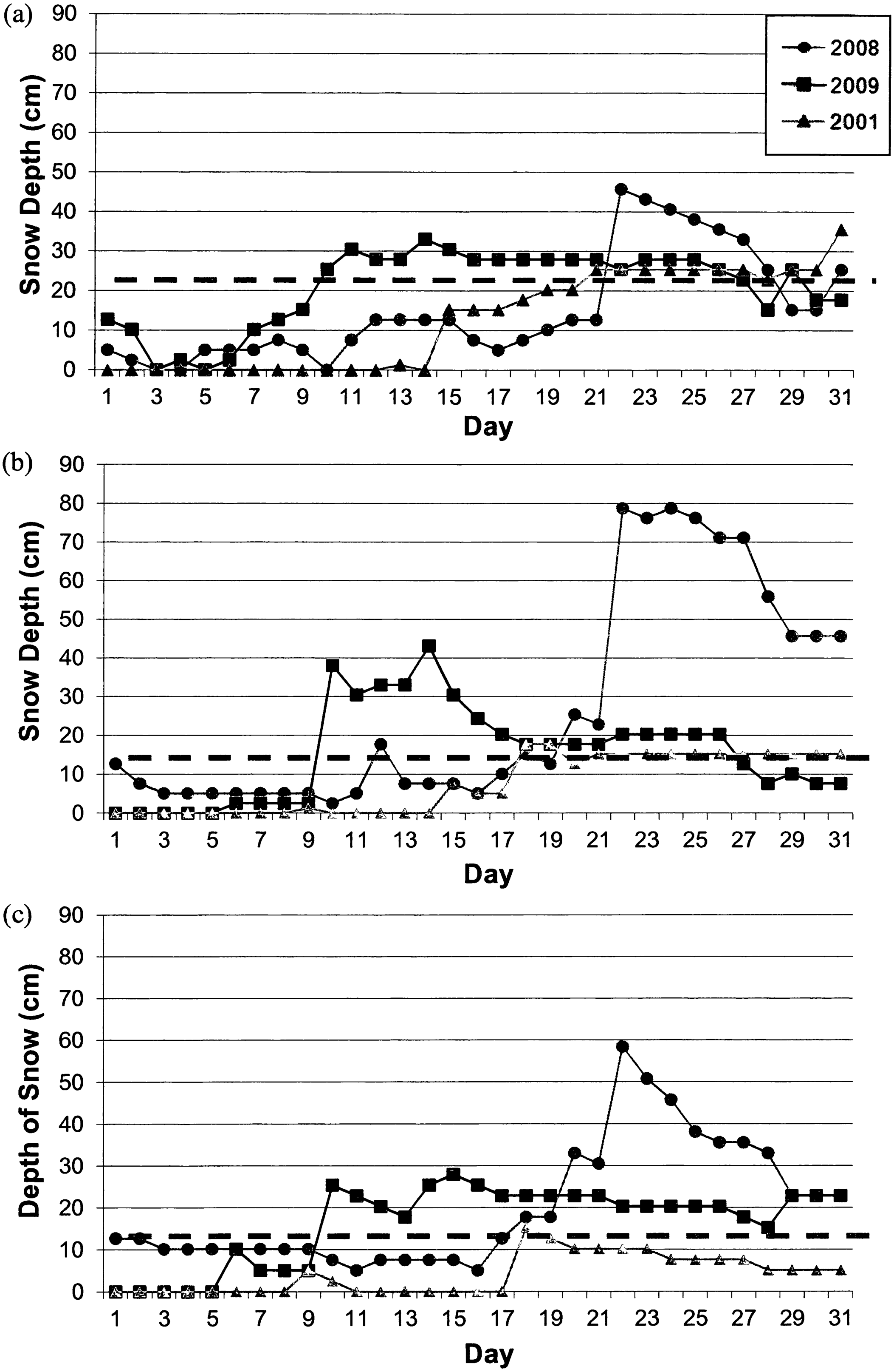

Figure 3-4. Daily snow depth (cm) in the CT Lakes (a), North (b), and White Mountain (c) regions, December 2001, 2008, and 2009. The dashed lines represent average snow depth for each region.

3-2); mean snow depth was >20 cm in 2001 (Fig. 3-2). Mean monthly temperature was 15-30° C in summer (June-August) (Table 3-1) and precipitation was within the normal range for the region each year. Mean monthly temperature was >0° C during the fall questing period (September-November) (Fig. 3-3); mean December temperature was <0° C and warmest in 2001 (Fig. 3-3). Permanent snow cover was earliest in 2009 (10 December), 2008, and 2001, respectively; there was no snow cover until 15 December in 2001 (Fig. 3-4).

White Mountain

Mean April temperature was >5° C each year, and was coldest in 2001 (5.7° C, Fig. 3-1). Mean snow depth in April was minimal in 2009 and 2010, but >25 cm in 2008 and 2001 (Fig. 3-2). Mean monthly temperature was 15-30° C during summer (June-August) (Table 3-1) and precipitation was within the normal range for the region each year. Mean monthly temperature was >0° C during the fall questing period each year (Fig. 3-3); December was <0° C and warmest in 2001 (0.1° C, Fig. 3-3). The onset of permanent snow cover was delayed until 17 December in 2001 (Fig. 3-4).

Discussion

April weather influences survival of adult female winter ticks (Samuel 2004), summer weather influences reproduction and egg survival, and weather in fall-early winter (September-December) influences the length of the questing period and transmission rates to moose (Samuel 1989, Welch 1991). April weather was conducive to survival of adult female ticks in each region both years except in CT Lakes in 2008 (<4° C, snow >35 cm) (Fig 3-1, 2). Summer weather was conducive to reproduction and egg survival each year that records were examined. Fall weather (September-November) was conducive to continual questing by larvae both years (Fig. 3-3). However, no major moose die-off was evident either year of the study suggesting that these weather conditions, although generally favorable for reproduction and host transmission of winter ticks, did not produce high infestation levels. The only obvious difference between 2001 (year preceding moose die-off) and 2008-2010 occurred in December; temperature was higher (Fig. 3-3) and snow cover was minimal until 15 December (Fig. 3-4). Surprisingly, April conditions in 2001 were not conducive to abnormally high survival of winter ticks.

This analysis indicates that questing probably occurs through most of November and curtails by December when daily temperature is <0° C. Fluctuations in temperature in November-December would either curtail or extend the questing period. In fact the transmission period in 2001, based on temperature and snow cover, was longer than any year of the current study. Musante et al. (2010) noted that weather conditions in September-November 2001 were conducive to tick survival, and that temperature in December was >5° C above normal and snow cover was absent through mid-December. He attributed the epizootic to prolonged questing in December associated with warm temperatures and lack of snow. April temperature was lower and snow depth higher in both the CT Lakes and North in 2001 than any year of this study (Fig. 3-1, 2), indicating that survival of adult female ticks, hence egg production, should not have been high. Because spring conditions in 2001 were not conducive to adult tick survival, the length of the 2001 fall questing period appears to be the critical element that caused the tick infestation and moose die-off in spring 2002.

Tick related die-offs do not occur on an annual basis and are usually concurrent and widespread geographically (Timmerman and Whitlaw 1992, Samuel 2004) indicating that epizootics are influenced by large scale weather events outside normal conditions. This was likely true of the 2002 die-off which occurred in New Hampshire, Vermont, Maine, Alberta, Saskatchewan, Manitoba, and Minnesota (Samuel 2004). Warm, snowless conditions in December 2001 were abnormal for northern New Hampshire (Fig. 3-3, 4) and occurred throughout the Northeast and Minnesota (Table 3-2, Fig. 3-5).

Although weather appears to play an important role in the survival of winter ticks, it should not be considered solely. Wilton and Garner (1993) suggested that tick abundance was related to the previous year's mean April temperature and survival declined when ambient temperature was <3-4° C. April temperatures were near or below this level in 2008 and 2009 in the CT Lakes region and well above it in the White Mountain region (Fig. 3-1), and all weather data suggest that the White Mountain region is more conducive to tick survival than the CT Lakes region. However, because index values were always higher in CT Lakes, other factors such as moose density likely influence tick abundance because moose density in the CT Lakes is >2X that in the White Mountain.

Although several studies indicate that April snow cover and temperature are related directly to occurrence of epizootics (Drew and Samuel 1986, Wilton and Garner 1993, Samuel 2007), December conditions that extended questing and

Table 3-2. Average temperature and rankings for Northeastern states, December 2001. Rankings are for 107 years between 1895 and 2001(1 = coolest; 107 = warmest) (Northeast Regional Climate Center).

State	Temp (° C)	Rank
New Hampshire	0	107
Maine	-2	106
Vermont	-1	107
Massachusetts	2	105
New York	1	107

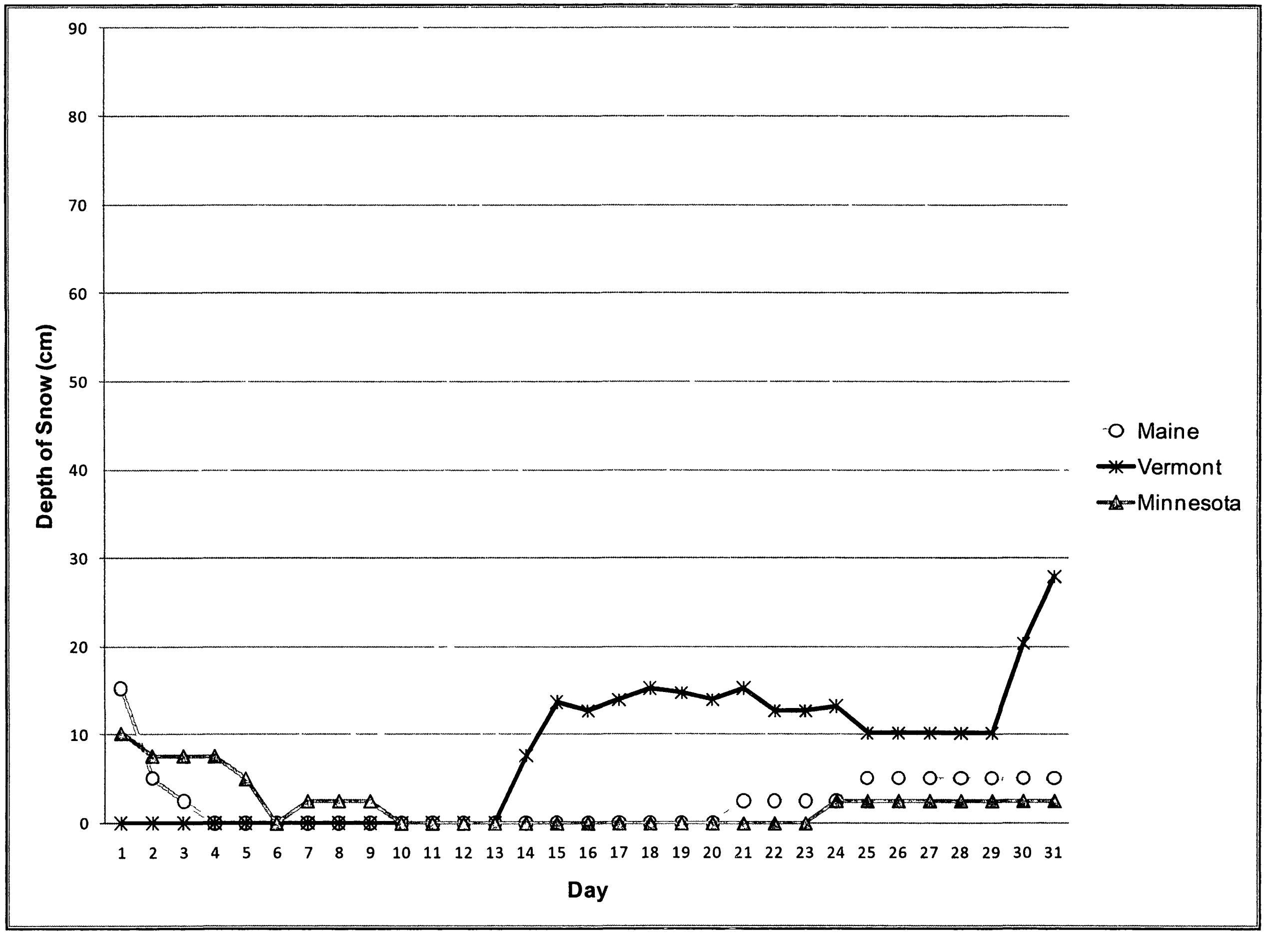

Figure 3-5. Daily snow depth (cm) measured in Maine, Vermont, and Minnesota, December 2001.

transmission were arguably more influential in the 2002 regional epizootic. April weather may be more important in northern latitudes where questing rarely extends into December. Further, openings such as clear-cuts and slope and aspect create microclimatic differences that influence survival and activity of winter ticks, and may be dissimilar to regional weather conditions. At the southern range of moose, as in New Hampshire, temperature and snow cover are presumably more variable in spring and fall and either/both influence relative tick abundance; therefore, monitoring of conditions in both seasons is warranted.

The current (2010) year's data indicate that tick loads in New Hampshire could be high in spring 2011. In all regions, April temperature was higher (Fig. 3-1) and snow depth lower than in any year studied (Fig. 3-2), and September-November temperatures were conducive for normal questing activity (Fig. 3-3). Further, ticks counted on harvested moose in 2010 were at their highest level in 3 years (Fig. 1-2). Assuming that the length of the questing period is most influential, the temperature and snow cover in December may dictate the severity of infestation in spring 2011. It will be important to conduct hair-loss surveys in the CT Lakes and North regions to assess and possibly provide a reference HLI level for an epizootic, and/or indicate the influence of temperature and snow cover in December on tick loads.

This study and others (Drew and Samuel 1986, Timmerman and Whitlaw 1992, Wilton and Garner 1993, Samuel 2004) indicate that weather is an important factor in tick abundance and distribution; therefore, climate change will probably affect occurrence and frequency of future tick epizootics. Mild late winter and early spring temperatures with low precipitation are beneficial to survival of winter ticks

(Samuel 2007), and one predicted consequence of climate change is an increase in average monthly temperature and shorter winters and earlier springs in New Hampshire (Intergovernmental Panel On Climate Change 2007). In New Hampshire annual temperature and precipitation have increased (4.6° C and 2.5%) since 1895, and snowfall has declined by nearly 15% since 1953 (NERAG 2001). The New England Regional Assessment uses 2 different models to predict more localized effects of climate change; both models predict an average increase in annual maximum temperature of 1.5° C by 2030 and 2-5° C by 2100. These temperature shifts will likely extend the activity periods of winter ticks, and ultimately increase tick survival, tick loads, and frequency of epizootics.

Increased occurrence of epizootics could cause relatively abrupt and perhaps permanent decline in regional moose populations. Therefore, it is important to monitor relationships among winter ticks, weather, and moose in New Hampshire to best develop adaptive management responses. Spring and fall weather should be monitored with focus on unusual conditions that may lead to high tick loads and epizootics, particularly April conditions with mean temperature >4° C and absence of snow cover, coupled with warm Decembers with late/no snow cover. Weather data should be compared to indices of tick abundance developed from tick loads of harvested moose and spring hair-loss surveys to further identify weather conditions that are related to epizootics.

CHAPTER 4

INFLUENCE OF MOOSE POPULATION DENSITY ON FOREST REGENERATION

Introduction

Moose are economically and ecologically important in northern New Hampshire with moose viewing a popular attraction and 521 hunting permits issued statewide in 2009 (2009 New Hampshire Wildlife Harvest Summary). Wildlife-associated recreation contributed ~$560 million to New Hampshire's economy in 2006 (USFWS 2006), and moose related activities represent a substantial portion of this figure. However, the forest industry is arguably the primary contributor to northern New Hampshire's economy. According to the Governor's New Hampshire Forest Products Industry Task Force Report (2008), the state generates over $2.3 billion annually from forest-based manufacturing and forest-related recreation and tourism. In 2003 International Paper Company sold 171,326 acres of commercial forestland to the Trust for Public Lands, permanently protecting this land for recreation and timber management (Staats and Kelly 2006). The majority of this land is managed by the Connecticut Lakes Timber Company (CLTC) through a working forest conservation easement with the New Hampshire Fish and Game Department (NHFG).

Adult moose require substantial browse to maintain such large body size (Bubenik 1997), and thus have the ability to considerably impact plant communities (Bowyer et al. 1998); high-density populations can have deleterious effects on preferred plant species (Peek 1997). Commercially managed forests create preferred habitat and forage for moose (Westworth et al. 1989, Scarpitti et al. 2005), and impact on forest regeneration has been documented across moose range. For example, browsing in Isle Royale National Park, Michigan prevented preferred species such as aspen (*Populus spp.*), birch (*Betula spp.*) and balsam fir from reaching the overstory and allowed spruce (*Picea spp.*) biomass to increase (McInnes et al. 1992). Sites with traditionally low moose densities and older sites with unreachable foliage and twigs escaped damage. In Russia high moose densities retarded growth of preferred forage species such as aspen causing rapid over-growth of spruce (Abaturov and Smirnov 2002), and in Finland browsing reduced preferred species and released conifers from competition; however, study sites were in wintering areas where moose concentrate in above average density (Heikkila et al. 2003). High winter densities of moose retarded growth of birch and killed some regeneration in Newfoundland (Bergerud and Manuel 1968), and reduced winter browse availability in winter deer yards in northern New Hampshire (Pruss and Pekins 1992). Little attention has been paid to the impact of moose browsing on forest regeneration in northern New Hampshire despite the year-round importance of early-successional browse to moose, and the importance of sustaining commercial forests (Scarpitti et al. 2005).

In the late 2000s the CLTC raised concern about the negative impact of moose browsing on regeneration of commercial tree species and its associated impacts on the economic viability of timber resources on the property. Due to the importance of both moose and the timber industry in northern New Hampshire, and the ability of moose to negatively impact forest regeneration, concern exists about providing optimal recreational opportunities and maintaining economically viable timber operations. This research was designed to evaluate the impact of moose browsing on regeneration of commercial tree species in 3 regions of different moose density in northern New Hampshire.

Methods

Regeneration surveys (Leak 2007) were performed in clear-cuts ≥2.83 ha (7 acres) in June-August 2009. Cuts were separated into 4 age classes in each region (0-5, 6-10, 11-15, and 16-20 years old) in order to gauge temporal changes across 20 years of growth. This time frame encompassed both the period of typical browsing and at least 10 years post-browsing. Seven to 10 cuts of each age class were located from timber harvest maps and spread throughout each of the 3 sample regions.

Small-plot surveys using milacre plots (~ 2.3 m diameter circle) were used to collect data. To avoid repeat measurements, plots were evenly spaced on equidistant transects throughout each clear-cut (Fig. 4-1). Approximately 75-250 small-plot surveys were conducted in each clear-cut providing approximately 700-1,000 plots/age class per region.

In each plot the dominant stem (tallest tree) was recorded as a commercial or non-commercial species. If the dominant stem was non-commercial, the plot was searched for the presence of a commercial species (Appendix D); commercial species included oak (*Quercus spp.*), sugar and red maple, yellow and white birch (*B. papyrifera*), American beech, aspen, balsam fir, red spruce, hemlock, and white pine (*Pinus strobus*). Stem damage was assessed qualitatively as fork, broom, or crook (Fig. 4-2). Height of damage above or below breast height, number of forks and crooks, and severity of crook (based on angle) were also recorded.

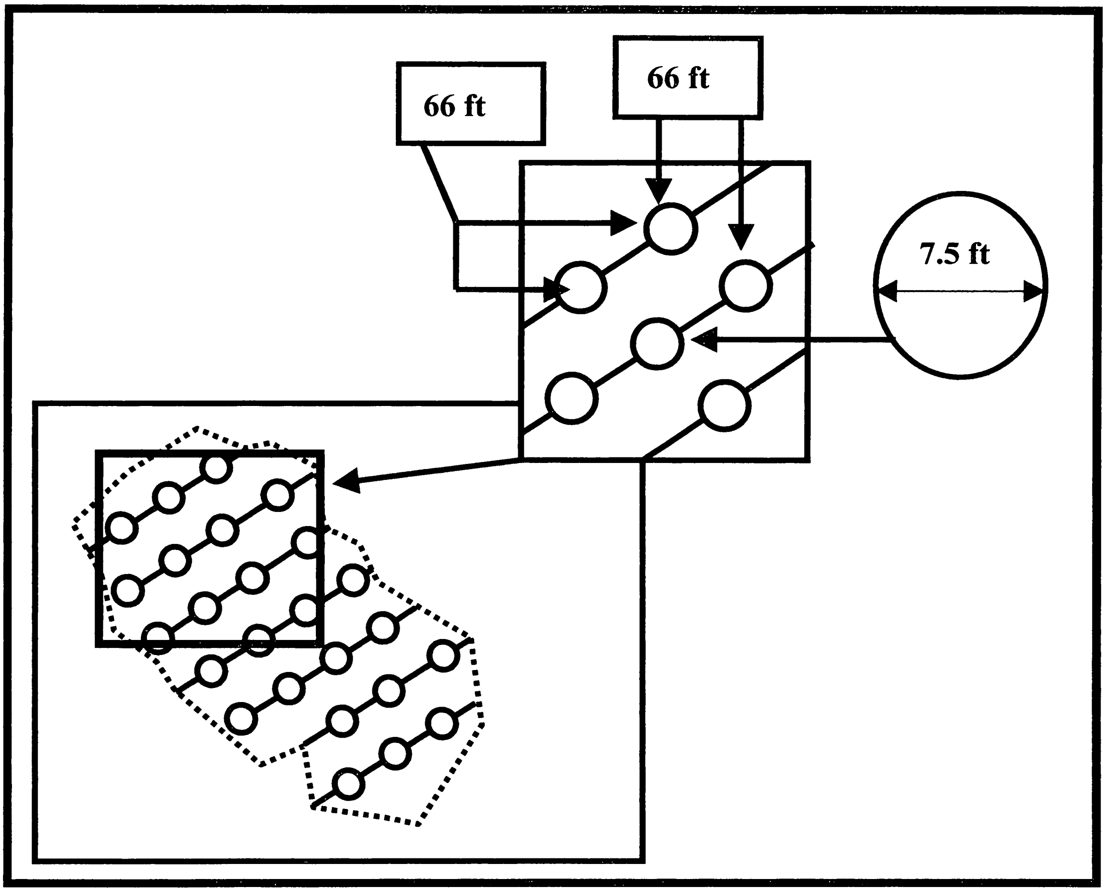

Figure 4-1. Selected clear-cut (≥2.83 ha) with equidistant transects upon which 75-250, 2.3 m radius plots were established to measure the presence of dominant commercial stems, stem quality, and relative height.

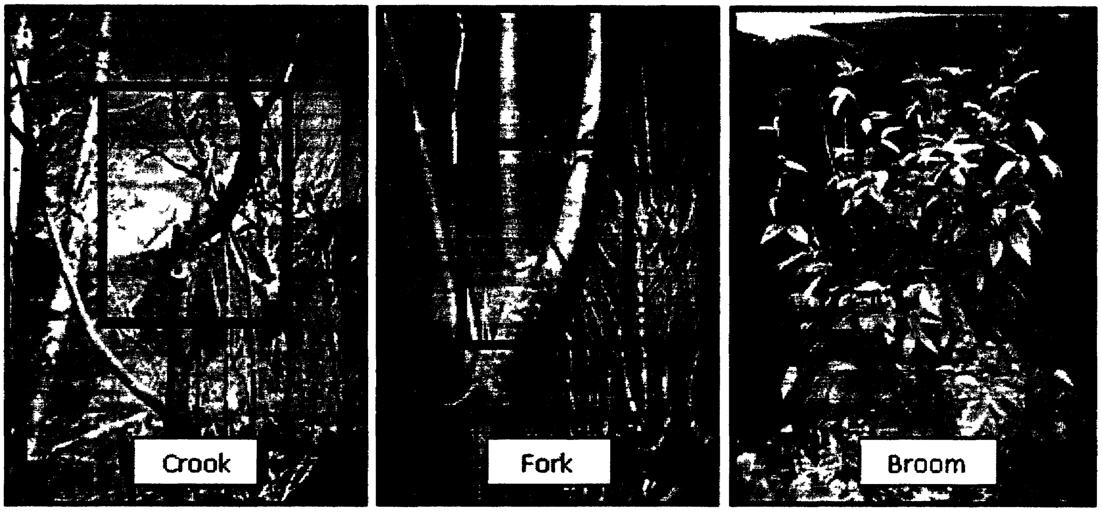

Figure 4-2. The 3 qualitative browse categories recorded for dominant commercial stems in each milacre sample plot. Height of damage above or below breast height, number of forks and crooks and the severity of the crook were recorded.

Browse defects that lead to classification as a severely damaged tree included broomed stems and multiple forks above breast height (~1.4 m).Damage not severe enough to affect tree quality included single forks and crooks; trees with such damage usually recover during subsequent growth (Switzenberg et al. 1955, Carvell 1967, Trimble 1968, Jacobs 1969). A minimum of 40-60% of sample plots should contain a commercial tree without severe damage to achieve a fully stocked stand at 80 years (Leak et al. 1987, Fig. 4-3).

The relative height of the dominant stem was estimated in the 3 older age classes to further assess browsing impact. The proportion of plots containing a dominant commercial stem ≥3.05 m (10 ft) without severe damage was used to compare relative height between age classes. Vegetation ≥3.05 m was presumed to be above the height of typical moose browsing (Bergstrom and Danell 1986).

Analysis of variance (ANOVA) was used to examine for differences in mean stocking rate of commercial trees, browse damage, and height of vegetation. Pairwise comparisons were made with Tukey's test. Significance for all tests was assigned a priori at $\alpha = 0.05$.

Results

Stocking rate of commercial trees was high (49-85%) in all age classes in each region, and increased with age class (Table 4-1). Stocking rate was 71-77% in each region by the 6-10 year age class, and ≥85% by the 16-20 year age class. The proportion of commercial trees with severe damage was low (<10%) in all regions and age classes except in the 11-15 year age class in the CT Lakes region (16%, Table 4-1). Severe damage in this age class was higher in the CT Lakes than the

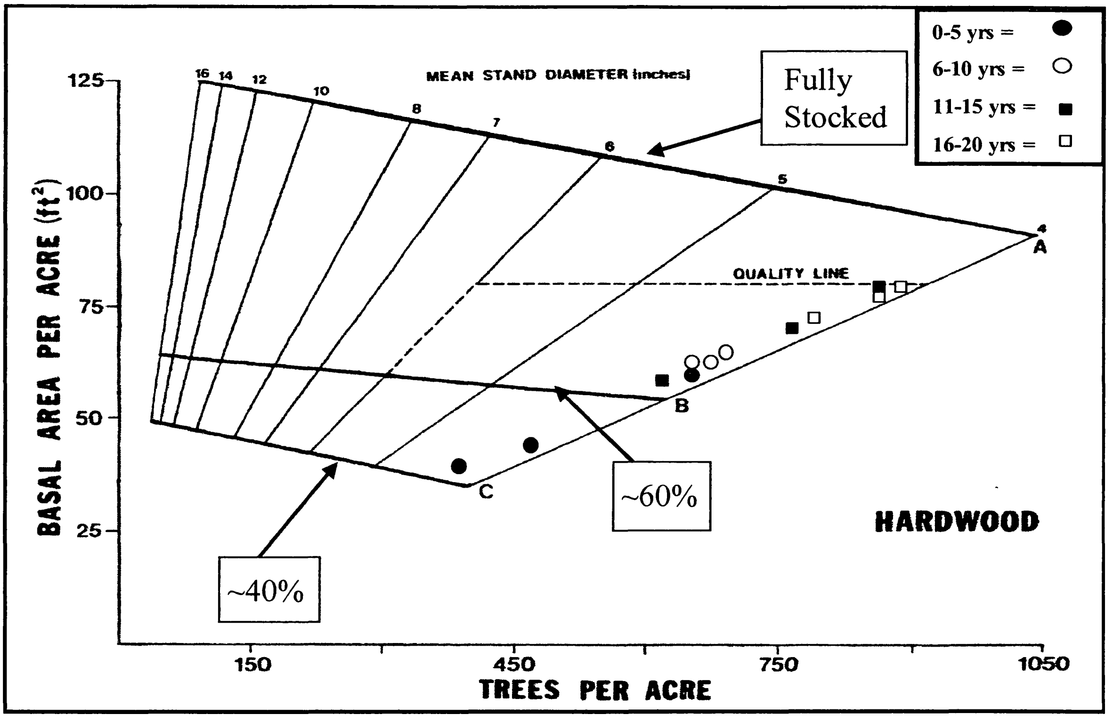

Figure 4-3. Stocking guides for main crown canopy of even-aged hardwood and mixed-wood stands. Shows basal area, number of trees per acre, and quadratic mean stand diameter. The A-line is fully stocked, the B-line is suggested residual stocking (~60%), and the C-line is minimum stocking (~40%) (Leak et al. 1987). The proportion (%) of commercial trees without severe damage are plotted by age class.

Table 4-1. Summary values of moose browsing indicating the stocking of commercial tree species, stocking of commercial trees with and without severe damage, and the proportion of commercial trees ≥3.05 m in height without severe damage (trees above this height were assumed to be released from browse) in clear-cuts in 3 regions of different moose density in northern, NH. Rows with unlike letters are statistically different ($P<0.05$).

Age Class	Stocking Rate Of Dominant Commercial Trees (%)	Stocking Rate Of Dominant Commercial Trees w/o Severe Damage (%)	Stocking Rate Of Dominant Commercial Trees w/ Severe Damage (%)	Proportion of Dominant Commercial Trees w/o Severe Damage and ≥3.05 m Tall (%)
CT Lakes				
0-5	49	47	2	N/A
6-10	77	69	8	22 (a)
11-15	78	61	16 (a)	43
16-20	87	78	9	63
North				
0-5	67	64	3	N/A
6-10	71	67	4	39 (ab)
11-15	86	85	1 (b)	69
16-20	87	85	2	70
White Mountain				
0-5	53	52	1	N/A
6-10	73	67	7	48 (b)
11-15	79	75	4 (b)	67
16-20	85	84	0	80

NA = not applicable

North and White Mountain regions (P = 0.00016 and 0.00581, respectively). The proportion of plots containing a commercial tree without severe damage was above the threshold stocking level of 40-60% in all age classes and regions, and generally increased with age class (Table 4-1, Fig. 4-3). The proportion of undamaged trees ≥3.05 m increased with age class in each region; for the most part, this proportion was inversely related to regional moose density (Table 4-1). Height in the 11-15 year age class was lower in the CT Lakes region than in the North (P = 0.005) and White Mountain regions (P = 0.016), and in the 6-10 year age class (P = 0.008) in the White Mountain region. Severe damage and population density were correlated (P = 0.0089), although damage was considered low overall in each region. Only 3 of the 116 clear-cuts (2.6%) were considered severely damaged. Two of these were in the 11-15 year age class in the CT Lakes region and 1 was in the 6-10 year age class in the White Mountain region. Stocking of commercial trees in these clear-cuts was ≤75% and >50% of these stems were severely damaged; damage to hardwoods was nearly 100% whereas damage to softwoods was minimal (Table 4-2).

Discussion

Moose browsing does not appear to be negatively impacting regeneration of commercial tree species in northern New Hampshire. Stocking rate of commercial tree species without severe damage was above the minimum threshold of 40-60% in all regions and age classes, and severe damage from browse was low in all regions and age classes (Table 4-1). Stocking rates in the 0-5 year age classes were lowest (49-67%) and was due to high stocking of non-commercial early successional species such as blackberry (*Rubus allegheniensis*), raspberry (*Rubus idaeus*), and pin cherry

Table 4-2. Summary values for 3 severely damaged clear-cuts in 2 sample regions in northern, NH indicating the stocking of commercial tree species, the proportion of commercial trees with severe damage, the proportion of commercial trees ≥3.05 m in height without severe damage (trees above this height were assumed to be released from browse), and the regional averages for these same values. Stocking of commercial hardwood and softwood species, and the proportion (%) of severe damage to hardwood and softwood species are also represented.

Sample Region and Age-Class	Stocking Rate Of Dominant Commercial Trees (%)	Proportion of Commercial Trees w/ Severe Damage (%)	Proportion of Dominant Commercial Trees w/o Severe Damage and ≥3.05 m Tall (%)	Hardwood Stocking (% Severe Damage)	Softwood Stocking (% Severe Damage)
CT Lakes					
11-15	69	63	16	72 (98)	28 (2)
11-15	75	52	22	75 (100)	25 (0)
Average	78	22	43	NA	NA
White Mountain					
6-10	69	52	16	99 (97)	1 (3)
Average	73	10	48	NA	NA

NA = not applicable

(*Prunus pennsylvanica*) and not heavy browsing. Severe browse damage in these age classes was only 1-3%, and stocking rate jumped to >70% by the 6-10 year age class (Table 4-1).

Relative height of trees increased with age class and was negatively correlated with moose density. Bergerud and Manuel (1968) noted that if browsing pressure is removed, "hedged" stems may escape and recover for harvest by a normal rotation time. One leader becomes apically dominant in forked stems (Jacobs 1969), and crooked stems straighten with added radial growth (Switzenberg et al. 1955, Trimble 1968). The increased height in regions with lower moose density is suggestive of a relationship between damage and moose density. However, because stocking rate was above the threshold level in all regions, and severe damage levels >10% occurred in only 1 age class in the CT Lakes, this relationship has negligible impact on regional forest productivity.

Browse damage was greatest in the 11-15 year age class in the CT Lakes region and higher than in the North and White Mountain regions (Fig. 4-4); however, the overall stocking level was above the threshold value. Two clear-cuts, one adjacent to a known moose wintering area, accounted for this difference. Moose often use traditional wintering areas to reduce movement and often concentrate in above average numbers (Renecker and Schwartz 1997). Heavy damage has been noted in areas with high winter densities in Finland (Heikkila et al. 2003) and Newfoundland (Bergerud and Manuel 1968), and measurable damage can occur in local areas. One additional clear-cut was severely damaged in the 6-10 year age class in the White Mountain region. No statistical difference in damage between region or age class

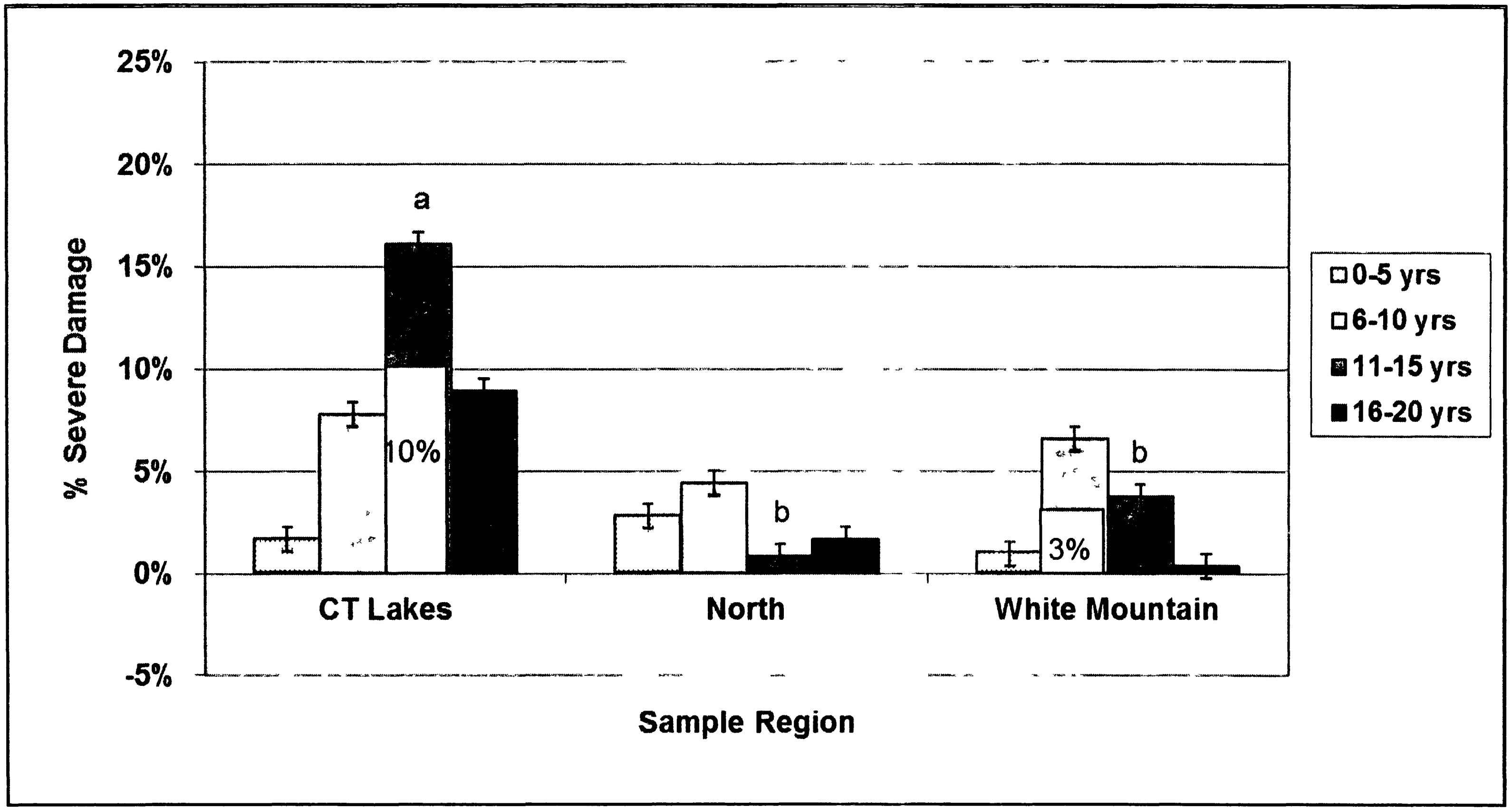

Figure 4-4. Proportion (%) of plots with severe damage in 4 age classes in 3 regions of northern, NH. The solid white bars represent proportions after 3 severely damaged cuts were removed from the data set (2 in CT Lakes and 1 in White Mountain region).

(Fig. 4-4) occurred after removal of these 3 cuts, indicating the importance of measuring and identifying local versus regional impacts.

Several studies have examined the impacts of moose density on tree species. In central Newfoundland winter densities of >4.6 moose/km^2 caused severe damage to balsam fir and white birch (Bergerud and Manuel 1968); a density of 2.32 moose/km^2 prevented serious damage of birch and fir (Bergerud et al. 1968). Angelstam et al. (2000) examined the effects of moose density across 3 geographic regions (Sweden, Finland, and Russian Karelia) with densities ranging from 0.2-1.7 moose/km^2, and found the proportion of severely damaged and dead stems increased 36-fold in the highest density region; regions with densities of ≤0.3-0.4 moose/km^2 had significantly lower damage. In Sweden, simulated browsing indicated that densities of 0.8-1.5 moose/km^2 should not have significant negative impacts on available winter browse, whereas densities of ≥2.0 moose/km^2 may (Persson et al. 2005). Faison et al. (2010) measured browse damage in southern New England at densities of 0.5-1.1 moose/km^2 and found only 3% of study sites were browsed intensively. Moose density in the study area in the previous 20 years was nearly double (~1.5-2.0 moose/km^2) that of current moose density (<1.0 moose/km^2 in all regions, K. Rines, NHFG, personal communication).

Although damage was low in all regions and age classes, severe browsing may shift local species composition. The 2 severely damaged cuts in CT Lakes were stocked predominately with deciduous species that had much higher damage relative to coniferous species (Table 4-2), suggesting that coniferous species may eventually dominate these stands. Intense browsing of preferred deciduous species allowed spruce biomass to increase in Isle Royale, Michigan (McInnes et al. 1992), and high browsing of preferred forage allowed rapid over-growth of spruce in Russia (Abaturov and Smirnov 2002). Severe browsing by moose does not appear to be shifting regional species composition. At least 3 commercial hardwood species and/or balsam fir account for ≥50% of the species composition in each age class in the CT Lakes and North regions (Appendix K, L), and the majority are classified as light-no damage. As softwoods are less common in the White Mountain region, one concern could be a shift toward beech dominance due to severe browsing of more preferred species; however, other commercial species accounted for 36-66% of the species composition and increased with age class (Appendix M). Further, the proportion of non-commercial species declined in each older age class in all regions.

Our results indicate that stocking rates of commercial tree species were above the threshold stocking level in all 3 regions. Moose density and browse damage appeared to be correlated; however, damage was low in each region at all moose densities. Severe browsing was site-specific and likely influenced by proximity to winter habitat; however, forest composition may shift to coniferous species in such situations. Severe browse damage does not appear to be shifting regional species composition. Measurements taken in the 0-5 year age class are most likely poor indicators of regeneration potential as the forest tends to compensate with additional growth. Presumably, evident heavy browsing in this young age class created the perception that regeneration and stocking would be impacted long term. This study indicates that measuring regeneration and stocking in older age classes provides a more accurate assessment of moose impact on forest productivity and accounting for moose population density and local impacts.

CONCLUSIONS

1. Based on measurements in 3-5 year old clear-cuts, tick abundance and regional moose density were correlated both years (2008 and 2009). Tick abundance was highly variable in clear-cuts in all regions and likely caused lack of statistical difference among regions and between years. The few cuts with high abundance (2-7X higher than regional mean) and the high variability suggests that winter ticks are not evenly distributed within this preferred habitat type, regardless of moose density. Therefore, the flagging technique is probably not practical to index tick abundance or tick loads, and it is also very labor intensive and costly.
2. Fewer ticks were counted on harvested moose in 2009 than 2008, whereas numbers were higher in 2010. These data were similar to field measurements that indicated reduction in tick abundance from 2008 to 2009. Calves had more ticks than adult moose (~2-6X) each year and bulls had more than cows (~1.5-4X). The abundance of ticks measured at 4 areas on the carcass at check stations was statistically related to tick abundance measured from digested hide samples taken from the same areas. Combining data from the 4 areas produced the strongest relationship ($r^2 = 0.80$). Transect counts on harvested moose at check stations is easy and efficient, and should continue to provide an index of relative tick abundance and tick load on moose. However, index values could be lower that actual tick loads if weather conditions extend the questing period into December. Collection of multiple years of data will be necessary to develop an effective index.

3. Spring hair-loss surveys conducted on road-side moose in April-May indicated a reduction in hair-loss from 2009 (HLI = 2.86) to 2010 (HLI = 2.50) based on combined regional data. Bulls had the highest HLI both years; however, there was little variation (2-16%) in the HLI of bulls, cows, and calves indicating that sex/age of moose has little influence on survey results. The HLI values were not associated with a documented tick epizootic or moose die-off during the study; therefore, continuing annual surveys is suggested to develop an effective index. The ability to document moose die-offs in New Hampshire is limited because little data is collected on moose mortalities. More detailed documentation of moose mortality in the state would help associate index values with related moose die-offs.
4. In the North region a single-day survey in May (n = 51) produced similar results (~4% lower) as the larger survey, suggesting that a single-day survey might suffice if an adequate sample size (~50) is realized. A regional survey should be conducted by the same person within a 5-day period (1 May-15 May) that is focused on the most commonly used roadside saltlicks in a region until ≥50 individual moose are observed. Surveys should be restricted to the CT Lakes and North regions only. Spring calf:cow ratios should be compared to those calculated from fall hunter surveys to gauge possible decline in calves associated with a winter tick related die-off.
5. The combination of fall tick counts on harvested moose and spring hair-loss surveys should prove useful and adequate to index winter tick abundance and tick loads in northern New Hampshire. They are both time and cost effective

and capable of indicating annual change in tick abundance. Check station counts provide an indication of transmission during the questing period, while hair-loss surveys should help confirm major mortality events in late winter-spring. Calf:cow ratios obtained during hair-loss surveys could prove useful in detecting years of high calf mortality. Because major tick related die-offs are usually concurrent and widespread geographically, tracking regional differences in New Hampshire may not be as important as obtaining adequate tick load samples from harvested moose and at least one regional hair-loss survey of ≥50 moose.

6. A continued decline in body weight and corpora lutea count of yearling cows has occurred from 1988-1998 to 2005-2009 in New Hampshire. Yearling ovulation rates dropped from 56 to 21% and the mean dressed body weight of cows is currently <200 kg; reproduction of cows <200 kg is minimal. Conversely, adult rates have remained normal (60-97%); rates and trends in Vermont were similar. This downward trend in yearling size and productivity, yet stable condition of adult moose, indicates that non-habitat related factors are probably impacting the productivity of regional populations. The lack of a documented winter tick epizootic and associated moose die-off since 2002 suggests that annual winter tick infestation of calves have measurable influence on calf survival and yearling growth and fecundity. Continued monitoring of physical parameters and productivity of harvested moose, particularly the yearling cohort, is warranted to assess the influence of winter ticks and habitat quality on regional moose populations.

7. Weather conditions, although generally favorable for reproduction and host transmission of winter ticks, did not appear to produce high infestation levels resulting in an epizootic. The only obvious weather difference between 2001 (year preceding documented moose die-off) and 2008-2010 occurred in December 2001 that had abnormally high temperature and lack of snow cover until 15 December. Because spring conditions in 2001 were not conducive to adult tick survival, the length of the 2001 fall questing period appears to be the critical element that caused the tick infestation and moose die-off in spring 2002. Fall and spring weather should be monitored with focus on unusual conditions that may cause high tick loads and epizootics, namely a warm December with late/no snow cover followed/preceded by a warm April (>4° C) without snow cover. Weather data should be compared to indices of tick abundance developed from tick loads of harvested moose and spring hair-loss surveys to further identify weather conditions that are related to epizootics. Temperature shifts related to climate change will likely extend the activity periods of winter ticks, and ultimately increase transmission and tick loads, survival of reproductive females, and frequency of epizootics.
8. Stocking rate of commercial tree species in clear-cuts aged 2-20 years old was well above stocking threshold values in all regions. Although moose density and browse damage were correlated, damage was low in each region at all moose densities. Severe browsing was site-specific (only 2.6% of clear-cuts), was likely influenced by proximity to traditional moose wintering areas, and may shift local species composition in favor of softwood. Severe browsing

does not appear to be shifting regional species composition. The 0-5 year old age class is not a reliable indicator of browsing impacts because compensatory growth occurs after a clear-cut ages and grows beyond use of moose, and commercial species do not necessarily dominate this age class. Measuring regeneration and stocking rate in older age classes provides a better assessment of impacts on forest productivity. The current stocking rate of commercial tree species indicates that browsing levels associated with the moose population density in the past 20 years has not measurably impacted forest productivity in northern New Hampshire.

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APPENDICIES

APPENDIX A. DATA SHEET FOR SAMPLING LARVAL TICKS IN CLEAR-CUTS.

Winter Tick Flagging Data Sheet

Sampler Name: ____________________

Date : ____________________

Weather: __________ **Temp:** __________ **Rel. Hum:** __________

Wind Speed: __________ **Wind Dir:** __________

Start Time: __________

End Time: __________

Flagging Key:

Visit 1	Visit 2	Visit 3	Visit 4	Visit 5	Visit 6
Blue (B)	Pink (P)	Yellow (Y)	Blue (B)	Pink (P)	Yellow (Y)

Sample Site: ____________________

Sample Region: ____________________

Start Coordinates: **East:** __________ **North:** __________

Start Bearing: __________ **90 deg Bearing:** __________

Start Transect: __________

End Transect: __________

Ticks Collected											
Transect #											
Transect Length											
Estimated # Ticks											

Total Area Sampled: ____________________

Comments:

APPENDIX B. DATA SHEET FOR SAMPLING TICKS ON HARVESTED MOOSE.

Check Station ____________________ **Date** ____________ **Sampler** __________________________

Seal #	Time of Death	Time Start (24)	Time End (24)	Ticks Leaving? None Few Many	Number of Ticks Per Transect															
					Neck				Rib				Rump				Shoulder			
					1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4

Comments (by seal number):

APPENDIX C. SPRING HAIR-LOSS SURVEY DATA SHEET.

(Front Side of Data Sheet)

Moose Hair-Loss Severity Survey

(Spring survey of winter tick induced hair-loss on moose)

Observer Name: ______________________

Hair-Loss -- N = none, L = light, M = moderate, S = severe, W = worst case
Sex -- C = cow, B = bull, U = unknown
Age -- A = adult, Y = yearling, C = calve, U = unkown age
WMU -- (A1, A2), (B, C1, C2, D1), (E1, E2, E3, D2, F)
Moose ID # -- Keep a running tally of all observed and recorded moose.
Please mark the onset of the natural spring moult in comments

See diagrams on reverse side

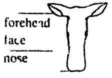
Picture -- If Picture taken check box. Label pictures and attach to data sheet. Label picture with Moose ID # - Date - Observer Initials. Ex. (1-4/20/10-DB)

(If GPS location: make sure you use NAD 83 and UTMs)

Date (mm/dd/yy)	Time (24.00)	Hair-Loss	Sex	Age	WMU	Town	Exact Location (GPS/Description)		Comments	Moose ID #	Picture

APPENDIX C. (CONTINUED).

Figure 1



Helpful Hints

To Distinguish Sex in adults (fig 1) compare the color of the face to that of the forehead if they are uniformly brown it is probably a cow if the face is darker than the forehead it is probably a bull In young & adults most cows have a white patch of hair (6 x 6) directly under the tail

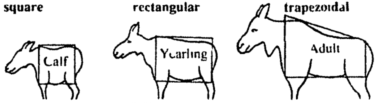
To Distinguish Age

1 Body Shape

Calves bodies are **square**

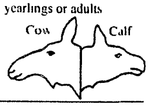
Yearlings are **rectangular**

Adults are **trapezoidal**



2. Facial Characteristics

Calves faces are shorter & their noses smaller than yearlings or adults

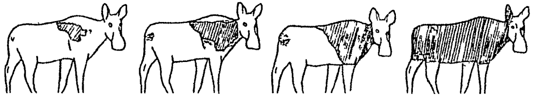


Tick Infestation

▨ Hairless or practically hairless area often scabby with much broken hair

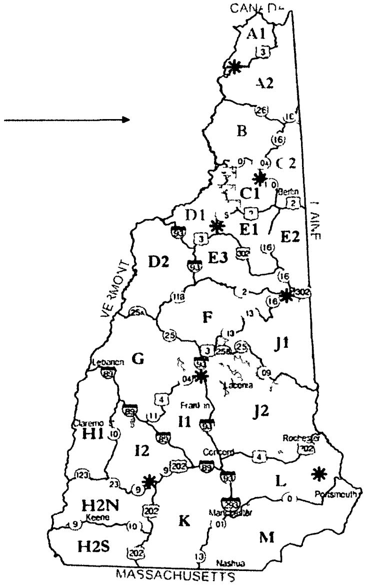
☐ Some hair loss Looks patchy

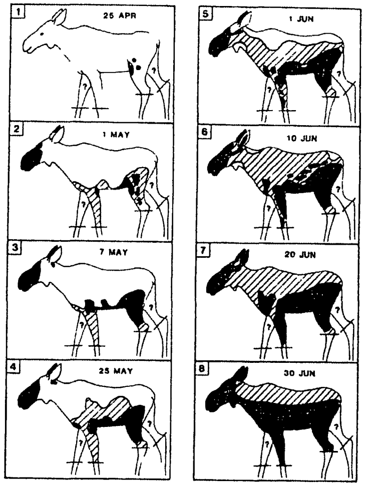
Tick Induced Hair-Loss Pattern →



Light Infection · Moderate Infection · Severe Infection · Worst Case

WMUs →





☐ Winter Hair (pile and fur)

▨ Winter Hair (pile)

■ Summer Hair

← **Natural Spring Moult Pattern**

On set of the spring moult will be noticable when moose begin to lose hair on stomach

(Dates on diagram are for moose observed in Alberta Canada)

APPENDIX D. REGENERATION SURVEY DATA SHEET.

Regeneration Survey Data Sheet

Page: **Of:**

Observer: **Cut ID:** **Cut Year:**

Date : **Region:** **Cut Size:**

Start Time: **End Time:**

Start Coordinates: **East:** **North:** **Start Bearing:** **90°:**

Plot #													
Commercial													
Damage													
Height													
Non-Commercial													
Damage													
Height													

Comments:

Plot #													
Commercial													
Damage													
Height													
Non-Commercial													
Damage													
Height													

Comments:

APPENDIX E. MEAN (±SD) FIELD-DRESSED BODY WEIGHT (kg) OF COW MOOSE IN 3 SAMPLE REGIONS AND STATEWIDE IN NEW HAMPSHIRE AND STATEWIDE IN VERMONT, AND MAINE, 1988-2009. VERMONT DATA ARE FROM 1993-2009.

Parameter	0.5 yr		1.5 yr		2.5 yr		3.5 yr		4.5 yr		5.5 yr		≥6.5 yr	
	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean
1988-1998														
CT Lakes	22	111±25.6	58	214±31.5	64	257±38.1	44	264±33.1	17	271±39.3	21	259±31.1	40	264±39.1
North	14	104±18.6	56	217±25.2	37	254±30.4	23	261±33.5	20	277±33.3	6	297±26.1	26	263±26.5
Whites	22	117±29.2	38	212±33.7	37	243±29.3	18	251±37.8	7	268±28.8	9	263±32.0	22	254±43.0
Statewide	74	110±25.0	175	211±30.9	167	258±314.3	102	255±34.8	55	268±34.0	46	261±32.1	106	258±35.6
Vermont	10	103±19.30	45	203±30.30	35	253±23.62	22	256±33.07	10	259±20.10	9	248±40.58	24	259±33.22
Maine	44	111±19.2	186	198±30.6	207	249±34.4	150	259±32.5	110	270±30.2	71	271±27.6	187	267±36.5
1999-2004														
CT Lakes	17	110±20.1	96	203±27.8	47	252±25.3	30	248±30.0	20	267±26.9	12	252±42.9	34	258±25.6
North	8	104±21.1	41	207±25.4	37	255±30.8	25	254±30.5	15	279±23.6	10	272±28.1	46	274±31.8
Whites	9	105±17.9	20	198±27.7	12	254±17.3	10	239±25.3	10	272±46.3	12	262±25.5	16	258±32.2
Statewide	51	105±20.1	206	203±27.0	132	250±28.7	85	246±29.1	68	263±34.7	48	260±31.5	133	263±31.4
Vermont	37	99±21.59	131	196±25.21	116	245±26.60	75	256±30.76	54	263±31.26	41	267±31.73	150	265±33.77
Maine	78	115±30.2	330	205±27.3	353	262±30.5	235	273±30.5	152	273±28.2	102	270±30.6	409	275±34.0
2005-2009														
CT Lakes	14	108±25.5	66	192±28.4	39	239±37.4	30	265±23.2	21	234±46.7	10	250±35.7	34	257±42.5
North	18	109±18.1	51	196±29.0	35	246±26.6	28	265±33.1	20	263±35.4	8	246±38.2	49	262±33.2
Whites	5	101±13.7	17	181±30.6	17	240±27.4	11	240±33.0	5	230±63.4	8	241±26.9	12	243±34.0
Statewide	45	107±22.0	165	190±29.3	117	238±31.0	87	258±31.0	60	24743	40	246±28.6	131	257±36.4
Vermont	104	100±19.20	219	185±26.91	162	236±33.96	155	248±31.66	105	251±31.58	74	245±31.48	255	255±37.41
Maine	43	122±19.2	238	205±29.4	224	257±27.5	176	268±31.6	122	269±27.5	93	268±33.7	356	273±35.3

APPENDIX F. MEAN (±SD) CORPORA LUTEA (CL) AND OVULATION RATE (%) OF COW MOOSE IN 3 SAMPLE REGIONS AND STATEWIDE IN NEW HAMPSHIRE AND STATEWIDE IN VERMONT, AND MAINE, 1988-2009. VERMONT DATA ARE FROM 1993-2009.

	1.5 yr			2.5 yr			3.5 yr			4.5 yr			5.5 yr			≥6 5 yr		
Parameter	n	Mean CL	Ovulated	n	Mean CL	Ovulated	n	Mean CL	Ovulated	n	Mean CL	Ovulated	n	Mean CL	Ovulated	n	Mean CL	Ovulated
1988-1998																		
CT Lakes	59	0.61±0.64	53	68	1.37±0.57	96	45	1.33±0.56	98	19	1.63±0.68	95	20	1.30±0.57	95	37	1.49±0.73	89
North	60	0.65±0.63	58	37	1.24±0.89	86	24	1.33±0.56	96	22	1.45±0.67	95	9	1.56±0.73	89	29	1.72±0.59	100
Whites	44	0.80±0.70	64	38	1.26±0.50	97	18	1.22±0.81	83	10	1.60±0.70	100	9	1.56±0.53	100	21	1.10±0.77	81
Statewide	187	0.65±0.65	56	174	1.26±0.66	91	102	1.29±0.62	93	62	1.53±0.65	97	46	1.37±0.61	93	108	1.46±0.73	90
Vermont	25	0.36±0.49	36	18	1.06±0.42	94	10	1.20±0.42	100	6	1.33±0.52	100	4	1.25±0.96	75	13	1.46±0.52	100
1999-2004																		
CT Lakes	95	0.35±0.52	33	56	1.09±0.55	91	31	1.23±0.67	87	21	1.19±0.60	90	14	1.36±0.84	79	41	1.22±0.57	93
North	41	0.44±0.55	41	37	1.08±0.55	89	29	1.17±0.66	86	16	1.38±0.50	100	10	1.10±0.74	80	49	1.31±0.62	92
Whites	23	0.43±0.51	43	16	1.13±0.34	100	11	1.09±0.54	91	13	1.23±0.60	92	14	1.36±0.50	100	21	1.38±0.67	90
Statewide	200	0.42±0.52	41	142	1.09±0.53	91	90	1.17±0.60	89	72	1.26±0.56	94	54	1.30±0.63	91	151	1.31±0.60	93
Vermont	65	0.26±0.44	26	72	1.07±0.56	88	40	1.03±0.48	90	36	1.08±0.50	92	23	1.41±0.59	96	80	1.30±0.60	95
2005-2009																		
CT Lakes	66	0.21±0.45	20	42	1.05±0.49	90	32	0.94±0.56	81	23	0.83±0.58	74	11	1.36±0.81	91	37	1.03±0.64	81
North	58	0.21±0.41	21	37	0.92±0.43	86	30	1.23±0.50	97	21	1.05±0.67	81	13	0.92±0.64	77	53	1.19±0.65	91
Whites	16	0.19±0.40	19	21	0.95±0.50	86	12	1.08±0.51	92	5	0.60±0.55	60	9	1.00±0.50	89	15	1.07±0.59	87
Statewide	169	0.21±0.42	21	127	0.98±0.48	87	91	1.08±0.54	89	62	0.98±0.61	81	48	1.13±0.67	88	142	1.13±0.66	86
Vermont	99	0.16±0.37	16	67	0.99±0.59	82	81	0.98±0.59	81	45	1.02±0.40	93	40	0.95±0.50	85	123	0.96±0.56	82

APPENDIX G. MEAN (±SD) FIELD-DRESSED BODY WEIGHT (kg) OF BULL MOOSE IN 3 SAMPLE REGIONS AND STATEWIDE IN NEW HAMPSHIRE (1988-2009) AND STATEWIDE IN VERMONT (1993-2009).

	0.5 yr		1.5 yr		2.5 yr		3.5 yr		4.5 yr		5.5 yr		≥6 5 yr	
Parameter	n	Mean Weight	n	Mean Weight	n	Mean Weight	n	Mean Weight	n	Mean Weight	n	Mean Weight	n	Mean Weight
1988-1998														
CT Lakes	19	130±23.0	80	232±42.8	78	278±46.4	43	322±37.9	42	347±41.0	28	367±32.9	43	361±39.2
North	15	118±25.6	119	223±29.7	112	273±39.0	70	314±30.3	54	338±36.9	37	352±38.0	47	349±36.3
Whites	17	115±17.9	102	222±44.1	91	271±40.3	69	314±39.0	69	332±41.7	21	351±37.9	44	361±35.2
Statewide	67	119±22.8	377	222±38.8	361	271±41.5	229	311±35.6	174	335±39.8	108	350±36.7	180	352±37.1
Vermont	21	118±22.5	58	216±27.3	52	273±27.0	23	314±39.8	23	346±42.2	11	356±36.1	36	363±41.1
1999-2004														
CT Lakes	17	114±24.9	44	209±25.7	41	272±30.8	43	301±33.6	37	335±33.2	11	347±35.4	43	352±36.1
North	10	111±24.2	80	212±22.7	71	267±24.0	76	298±28.0	50	322±28.3	30	348±30.4	78	356±29.5
Whites	6	111±33.7	38	194±22.3	43	261±32.0	38	290±28.3	19	310±35.1	17	321±23.2	33	346±30.2
Statewide	42	114±25.6	235	206±24.5	246	262±28.3	251	294±29.8	172	317±32.4	96	331±31.6	243	344±31.6
Vermont	38	114±22.7	127	202±27.6	119	261±30.8	126	294±34.3	90	318±31.1	79	340±37.5	162	346±40.2
2005-2009														
CT Lakes	14	121±21.5	43	204±33.6	33	258±28.0	39	294±34.4	29	316±36.6	13	335±29.3	49	338±40.3
North	11	125±23.2	61	207±27.5	74	367±26.5	80	290±31.8	45	321±28.7	27	330±45.6	67	346±33.9
Whites	12	103±26.5	36	192±23.5	28	242±32.0	29	278±32.0	22	302±37.8	12	325±24.2	24	341±34.1
Statewide	46	115±25.0	184	201±29.1	219	253±29.6	214	284±32.8	150	312±33.9	93	319±37.4	218	335±36.2
Vermont	87	114±16.4	247	196±27.1	222	253±33.7	189	280±33.4	145	312±36.5	107	329±40.0	278	333±37.0

APPENDIX H. MEAN (±SD) ANTLER POINTS OF BULL MOOSE IN 3 SAMPLE REGIONS AND STATEWIDE IN NEW HAMPSHIRE (1988-2009) AND STATEWIDE IN VERMONT (1993-2009).

	1.5 yr		2.5 yr		3.5 yr		4.5 yr		5.5 yr		≥6.5 yr	
Parameter	n	Mean Points	n	Mean Points	n	Mean Points	n	Mean Points	n	Mean Points	n	Mean Points
1988-1998												
CT Lakes	84	6±2.8	84	10±4.2	47	13±4.2	45	15±4.0	31	17±4.7	47	17±4.7
North	133	5±2.6	122	10±3.6	79	13±4.4	58	14±4.2	38	17±4.8	53	16±5.0
Whites	115	6±3.4	106	9±4.7	79	13±3.8	47	14±4.3	28	15±4.4	56	17±4.2
Statewide	411	5±2.9	395	9±4.2	258	12±4.41	190	14±4.2	122	16±4.7	215	16±4.6
Vermont	61	5±2.7	52	10±2.7	23	12±2.8	25	15±4.1	12	16±3.8	36	18±3.9
1999-2004												
CT Lakes	47	5±3.1	45	10±3.3	52	12±2.8	45	15±4.8	11	15±3.5	47	18±4.9
North	96	5±1.9	77	10±2.7	91	12±3.5	57	14±3.6	34	17±4.1	81	18±4.2
Whites	42	4±1.4	53	9±3.3	49	11±3.9	24	13±3.9	25	17±3.8	44	15±4.3
Statewide	259	5±2.2	276	9±3.1	294	11±3.5	195	13±4.2	114	15±3.9	268	16±4.5
Vermont	126	5±2.2	128	9±2.9	131	11±3.6	93	14±3.7	79	15±4.5	169	16±4.4
2005-2009												
CT Lakes	46	4±1.7	37	8±2.8	41	11±3.4	31	13±4.8	16	16±4.7	55	16±4.1
North	66	4±1.6	79	9±3.9	86	11±3.7	50	13±3.4	29	15±4.3	70	16±4.6
Whites	39	4±1.8	34	8±3.2	40	10±3.1	22	13±4.3	18	14±3.9	29	15±4.2
Statewide	197	4±1.7	249	8±3.0	243	11±3.5	163	13±3.9	106	14±4.2	238	15±4.4
Vermont	264	4±1.2	230	8±3.3	203	10±3.5	151	13±4.1	109	15±4.7	290	15±4.1

APPENDIX I. MEAN (±SD) ANTLER SPREAD (cm) OF BULL MOOSE IN 3 SAMPLE REGIONS AND STATEWIDE IN NEW HAMPSHIRE (1988-2009) AND STATEWIDE IN VERMONT (1993-2009).

	1.5 yr		2.5 yr		3.5 yr		4.5 yr		5.5 yr		≥6.5 yr	
Parameter	n	Mean Spread	n	Mean Spread	n	Mean Spread	n	Mean Spread	n	Mean Spread	n	Mean Spread
1988-1998												
CT Lakes	76	68±20.6	79	95±20.1	45	110±17.5	44	126±18.0	29	134±16.5	42	137±14.2
North	123	64±15.7	105	89±16.5	73	109±16.0	56	121±17.3	35	131±15.2	45	134±13.0
Whites	99	69±21.1	97	89±19.6	77	109±17.3	43	119±17.0	25	125±17.5	53	136±14.2
Statewide	372	66±11.2	363	90±10.7	246	107±15.2	183	120±16.5	114	126±16.5	197	133±14.7
Vermont	54	60±11.4	50	90±10.9	23	105±14.2	25	123±18.7	12	127±15.1	34	13715
1999-2004												
CT Lakes	44	60±14.0	45	89±12.7	52	100±17.3	45	118±20.6	12	126±11.2	47	136±18.5
North	96	59±12.2	76	87±9.9	87	100±12.7	54	116±12.4	34	128±11.9	82	137±14.0
Whites	40	57±10.7	53	83±12.4	49	98±14.2	25	110±13.7	25	124±13.5	45	130±14.7
Statewide	247	60±12.4	275	85±11.7	289	98±14.5	191	112±16.3	112	121±12.4	269	131±15.7
Vermont	118	60±11.8	126	82±11.6	128	97±14.6	94	107±15.0	79	119±20.4	165	129±18.1
2005-2009												
CT Lakes	44	59±10.2	39	82±12.7	40	101±15.2	30	113±19.6	16	132±20.6	53	131±15.0
North	63	57±10.7	77	84±10.2	87	99±15.5	47	110±13.7	29	123±14.2	70	132±14.5
Whites	39	59±13.2	34	81±9.4	40	96±14.7	21	104±16.5	18	122±15.2	28	127±14.7
Statewide	191	59±11.2	247	81±10.7	242	96±15.2	157	109±16.5	106	118±16.5	232	128±14.7
Vermont	247	56±12.4	224	79±14.7	199	92±15.3	148	104±18.6	107	114±17.9	282	122±18.0

APPENDIX J. MEAN (±SD) ANTLER BEAM DIAMETER (mm) OF BULL MOOSE IN 3 SAMPLE REGIONS AND STATEWIDE IN NEW HAMPSHIRE (1988-2009) AND STATEWIDE IN VERMONT (1993-2009).

	1.5 yr		2.5 yr		3.5 yr		4.5 yr		5.5 yr		≥6 5 yr	
Parameter	n	Mean ABD	n	Mean ABD	n	Mean ABD	n	Mean ABD	n	Mean ABD	n	Mean ABD
1988-1998												
CT Lakes	85	38±9.8	86	46±7.2	47	52±7.1	45	56±7.7	31	60±8.4	46	62±5.9
North	134	35±7.5	119	44±6.7	78	49±5.2	57	54±5.9	39	56±7.0	53	61±6.5
Whites	113	37±9.0	104	45±7.6	80	49±6.5	49	54±7.8	28	57±7.9	56	60±6.5
Statewide	415	36±8.7	391	45±7.2	258	49±6.3	191	54±7.2	124	56±7.8	214	60±6.3
Vermont	59	34±6.0	52	45±5.0	23	50±4.6	25	55±5.4	12	60±4.5	36	61±4.7
1999-2004												
CT Lakes	47	34±6.2	44	45±5.9	52	49±5.7	45	54±6.2	12	58±7.1	47	63±7.7
North	99	34±6.6	77	43±3.5	90	47±4.9	57	52±4.8	34	56±5.7	83	60±6.6
Whites	44	33±7.1	53	44±5.2	48	47±5.1	25	50±4.4	25	55±5.5	44	60±6.1
Statewide	262	34±6.6	275	44±4.7	291	47±5.2	195	51±5.5	114	54±5.9	271	59±6.9
Vermont	128	36±6.3	129	44±5.1	133	47±5.0	94	52±4.9	79	56±5.7	169	60±6.4
2005-2009												
CT Lakes	47	34±5.7	39	43±5.0	40	48±5.0	31	52±7.5	16	59±5.0	55	60±5.3
North	65	34±5.5	79	43±4.7	86	46±4.0	49	50±4.2	29	55±4.9	70	58±6.2
Whites	40	34±6.5	34	42±4.9	40	47±4.9	23	49±5.7	18	56±3.4	29	58±5.4
Statewide	199	34±5.8	251	42±4.8	243	46±4.5	162	50±5.7	106	54±4.7	236	58±5.7
Vermont	258	34±6.7	230	43±6.1	197	47±6.4	150	50±6 0	106	54±6.3	291	56±6.4

APPENDIX K. SPECIES COMPOSITION (%) AND BROWSE DAMAGE CATEGORY OF DOMINANT STEMS IN 6-10, 11-15, AND 16-20 YEAR OLD CLEAR-CUTS IN THE CT LAKES REGION.

Age Class	Species	Severe Damage	Moderate Damage	Light Damage	No Damage	Total
6-10						
	American beech	0	0	0	0	1
	Aspen spp.	1	1	3	1	5
	Balsam fir	0	1	4	16	22
	Red maple	1	2	3	1	6
	Red spruce	0	0	0	4	5
	Sugar maple	2	3	8	2	15
	White birch	3	1	4	2	9
	Yellow Birch	1	1	5	4	11
	Non commercial	NA	NA	NA	NA	27
11-15						
	American beech	0	0	1	1	2
	Aspen spp.	0	0	0	0	1
	Balsam fir	0	0	2	15	17
	Red maple	5	5	5	2	17
	Red spruce	0	0	0	4	4
	Sugar maple	0	2	2	1	6
	White birch	8	1	5	4	18
	Yellow Birch	4	2	5	3	14
	Non commercial	NA	NA	NA	NA	21
16-20						
	American beech	0	0	0	1	1
	Aspen spp.	0	0	1	0	1
	Balsam fir	1	1	1	23	26
	Red maple	1	2	7	3	12
	Red spruce	0	0	0	11	12
	Sugar maple	1	2	4	2	10
	White birch	4	2	6	3	15
	Yellow Birch	2	1	4	1	8
	Non commercial	NA	NA	NA	NA	14

APPENDIX L. SPECIES COMPOSITION (%) AND BROWSE DAMAGE CATEGORY OF DOMINANT STEMS IN 6-10, 11-15, AND 16-20 YEAR OLD CLEAR-CUTS IN THE NORTH REGION.

Age Class	Species	Severe Damage	Moderate Damage	Light Damage	No Damage	Total
6-10						
	American beech	0	1	4	3	7
	Aspen spp.	0	1	8	1	10
	Ash spp.	0	1	2	3	5
	Balsam fir	0	0	1	4	5
	Red maple	2	3	6	2	13
	Red spruce	0	0	0	0	1
	Sugar maple	1	2	7	1	11
	White birch	0	0	2	1	4
	Yellow birch	0	2	7	4	14
	Non commercial	NA	NA	NA	NA	30
11-15						
	American beech	0	0	0	0	0
	Aspen spp.	0	0	5	4	9
	Ash spp.	0	0	0	0	1
	Balsam fir	0	0	2	34	36
	Red maple	0	2	7	2	11
	Red spruce	0	0	0	5	5
	Sugar maple	0	1	3	0	4
	White birch	0	1	7	3	11
	White pine	0	0	0	0	0
	Yellow birch	0	0	4	3	8
	Non commercial	NA	NA	NA	NA	14
16-20						
	American beech	0	1	2	2	4
	Aspen spp.	0	0	4	2	6
	Ash spp.	0	0	0	0	0
	Balsam fir	0	1	3	33	36
	Red maple	1	2	9	1	13
	Red spruce	0	0	1	9	10
	Sugar maple	0	1	4	1	7
	White birch	0	1	5	1	8
	Yellow birch	0	1	2	1	4
	Non commercial	NA	NA	NA	NA	12

APPENDIX M. SPECIES COMPOSITION (%) AND BROWSE DAMAGE CATEGORY OF DOMINANT STEMS IN 6-10, 11-15, AND 16-20 YEAR OLD CLEAR-CUTS IN THE WHITE MOUNTAIN REGION.

Age Class	Species	Severe Damage	Moderate Damage	Light Damage	No Damage	Total
6-10						
	American beech	3	6	20	7	37
	Aspen spp.	0	0	2	1	3
	Ash spp.	0	1	4	3	8
	Balsam fir	0	0	0	0	0
	Oak spp.	0	0	0	0	1
	Red maple	0	1	4	1	5
	Red spruce	0	0	0	1	1
	Sugar maple	0	0	1	0	1
	White birch	0	2	7	3	12
	White pine	0	0	0	1	1
	Yellow birch	2	1	4	2	8
	Non commercial	NA	NA	NA	NA	23
11-15						
	American beech	1	4	18	5	29
	Aspen spp.	0	0	2	1	3
	Ash spp.	1	1	6	2	9
	Balsam fir	0	0	1	2	3
	Red maple	1	1	7	1	11
	Red spruce	0	0	0	2	2
	Sugar maple	0	0	2	0	3
	White birch	0	0	7	3	10
	Yellow birch	1	1	5	2	10
	Non commercial	NA	NA	NA	NA	19
16-20						
	American beech	0	2	12	4	18
	Aspen spp.	0	0	7	3	10
	Ash spp.	0	0	3	1	4
	Balsam fir	0	0	0	1	1
	Oak spp.	0	0	1	0	1
	Red maple	0	1	8	1	10
	Red spruce	0	0	0	1	1
	Sugar maple	0	0	2	0	3
	White birch	0	1	13	7	20
	White pine	0	0	0	0	0
	Yellow birch	0	1	9	5	16
	Non commercial	NA	NA	NA	NA	15