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

Daniel H. Bergeron[1,2], Peter J. Pekins[1], and Kristine Rines[2]

[1]Department of Natural Resources and the Environment, University of New Hampshire, Durham, New Hampshire 03824, USA; [2]New Hampshire Fish and Game Department, New Hampton, New Hampshire 03256, USA.

ABSTRACT: Biological data collected from harvested moose (*Alces alces*) were analyzed to assess whether temporal change has occurred in the physical and reproductive condition of moose from 1988–2009 in New Hampshire. Measurements included age and field-dressed body weight of both sexes, number of corpora lutea (CL) and ovulation rate of females, and antler beam diameter (ABD) and antler spread of males. Similar data were obtained from Maine and Vermont for comparative analysis. The only significant changes (P <0.05) occurred in the yearling age class: mean body weight of both sexes, number of CL, and ABD all declined in New Hampshire. The current ovulation rate (~20%) and mean body weight (<200 kg) of yearling females in New Hampshire and Vermont were considered low. The declines measured in yearlings, yet relative stability in adults, are consistent with the presumption that winter ticks (*Dermacentor albipictus*) impact the productivity of moose populations through reduced calf survival and growth and fecundity of yearlings. Density-dependent factors related to habitat change are also discussed given the recent, rapid expansion of moose in the 3 states. Continued monitoring of physical parameters and productivity of harvested moose, particularly the yearling cohort, is warranted to better assess the relationships among winter ticks, habitat quality, and moose populations.

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Age-specific body weight is directly related to the health and production of male and female moose (*Alces alces*) (Schwartz and Hundertmark 1993), and onset of ovulation in yearlings (Saether and Heim 1993). Antler measurements that are used routinely to estimate the health of white-tailed deer (*Odocoileus virginianus*) populations are also used to gauge population status of moose (e.g., Child et al. 2010); antler size in moose is influenced by many factors including nutritional status and health (Bubenik 1997). In New Hampshire, age, antler spread, antler beam diameter (ABD), number of points, corpora lutea (CL) count, and field-dressed body weight of hunter-harvested moose have been measured since 1988. Adams and Pekins (1995) found differences in body weight and number of CL in yearling cow moose relative to other age classes, but no difference within age classes from regions with different moose density. They concluded that yearling moose were useful for estimating herd health due to their substantial weight gain, change in antler characteristics, and onset of ovulation in this age class. Because their data were from a relatively new and expanding moose population in the 1980–1990s, they encouraged future analyses to assess both temporal and regional trends.

Musante et al. (2010) found that the ovulation rate and CL count of yearling moose in New Hampshire declined from

1988–1998 to 1999–2004, yet were unchanged in adults. In a comprehensive study including habitat use (Scarpitti 2006) and age-specific mortality rates, they concluded that epizootics of winter ticks (*Dermacentor albipictus*) caused periodic, annual high mortality in calves and lower fecundity in yearlings. Given the relationships between certain physical characteristics and nutritional status of a moose population, periodic analysis of physical and reproductive data should reveal trends and change in the relative condition of the moose population in New Hampshire. In this study we assessed temporal trends in physical characteristics and relative nutritional and reproductive status of moose in New Hampshire from 1988–2009, a period that encompassed previous studies (i.e., Adams and Pekins 1995, Musante et al. 2010) and 5 additional years. Further, we analyzed similar data from neighboring states Maine and Vermont to produce a regional assessment.

METHODS

Study Area

We used data collected by New Hampshire Fish and Game Department (NHFG) personnel at mandatory harvest check stations. Moose/data were from 3 northern regions that differed in moose population density (NHFG 2009) (Fig. 1); the 3 regions from highest to lowest density were Connecticut (CT) Lakes (0.83 moose/km^2), North (0.61 moose/km^2), and White Mountains (0.26 moose/km^2), respectively (K. Rines, unpubl. data, 2009).

Elevation in the study area ranges from ~120–1900 m, average snow depth ranges from 0–60 cm, and ambient temperature ranges from ~−30 to 30° C (NOAA 1971–2000). The CT Lakes and North regions were dominated by commercial hardwood species including sugar (*Acer saccharum*) and red maple (*A. rubrum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) tend to be the dominant species at higher elevations (>760 m) and in cold, wet lowland sites (Degraaf et al. 1992). These regions are predominately forested and the majority of the land is privately owned and commercially harvested using various silvicultural techniques (Degraaf et al. 1992); they contain ~10% wetlands and open water, and are interspersed with trails and logging roads.

The CT Lakes region is hilly with few high mountains, while the North is characterized by higher forested terrain. The White Mountains region contains the White Mountain National Forest which covers 304,050 ha and is ~97% forested. It contains the highest elevations in New Hampshire and 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 harvest in this region is at smaller scale than the other regions, with maximum clear-cut size of ~10–12 ha (DeGraff et al. 1992, Sperduto and Nichols 2004). White-tailed deer are sympatric with moose throughout the study area, and at low-moderate density (<4/km^2).

Field Measurements

Physical measurements of harvested moose in 1988–2009 were divided into 3 time periods (1988–1998, 1999–2004, and 2005–2009) and analyzed by region. Measurements included age and field-dressed body weight for both sexes, number of CL, ABD, antler spread, and number of points.

A micrometer was used to measure ABD 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 and sectioned later to

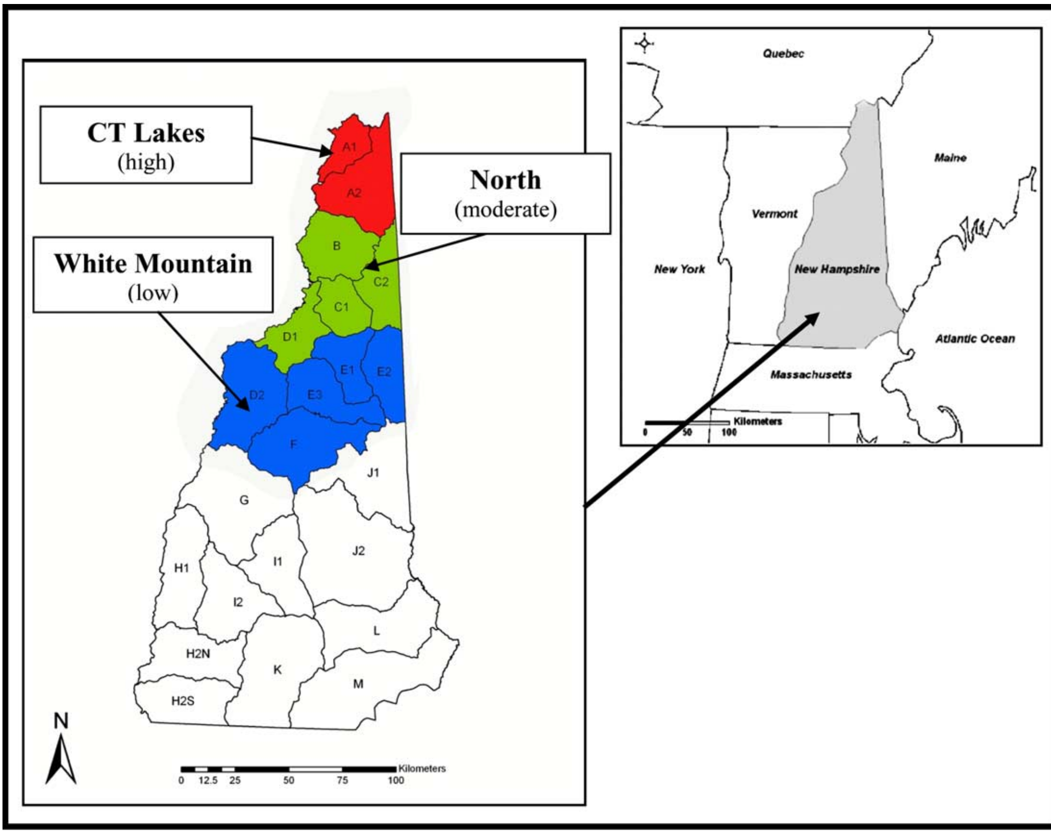

Fig. 1. Location of 3 study regions with different moose density (high-low) used to evaluate temporal trends in physical and reproductive status of moose in northern New Hampshire, 1988–2009.

visually count the number of CL (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; Maine data included only field-dressed body weight of cows and Vermont data were from 1993–2009.

Data Analysis

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. A Shapiro-Wilk test was used to test if the data were normally distributed and a Bartlett test was used to check for homogeneity of variance (Zar 1999). Pairwise comparisons were made with the Tukey test. Analyses were performed with Systat v. 13. Significance for all tests was assigned *a priori* at $\alpha = 0.05$.

RESULTS

The analysis included measurements from >3000 and 1500 male moose, and >1500, 1300, and 2500 female moose in New Hampshire, Vermont, and Maine, respectively. In New Hampshire, sample size was >10 in the middle age classes (1.5–3.5 years) in all regions in any given time period; sample size was >20 in all age classes/time periods for state comparisons.

Females

Statewide means for body weight and CL counts for all age classes are presented in Table 1. In New Hampshire the only significant differences between time periods in any region occurred in the yearling age class; albeit, body weight declined in most age classes in successive periods (Table 1). Body weight of yearlings declined significantly (~25 kg) from 1988–1998 to 2005–2009 in all regions (Fig. 2): CT Lakes (P = 0.033), North (P = 0.000), White Mountains (P = 0.003). The number of CL in yearlings also declined from 1988–1998 to 2005–2009 in all regions (Fig. 3): CT Lakes (43%, P = 0.009), North (68%, P = 0.000), White Mountains (76%, P = 0.003). The CL count was ~0.20 across all regions in 2005–2009, declining from 0.60–0.80 since 1988–1998. The ovulation rate in yearling cows declined from 56 to 21% from 1988–1998 to 2005–2009 in New Hampshire, and from 36 to 16% in Vermont. The average body weight of yearling cows with 0 CL 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), and CL counts, though not different, also declined to <0.20 (Fig. 3). The CL count was lower in Vermont than New Hampshire in 1988–1998 (45%, P = 0.030) and 1999–2004 (38%, P = 0.030) (Fig. 3); 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). 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). Mean body weight of Maine yearlings increased 9% from 1988–1998 to 2005–2009, and only Maine had a statewide mean >200 kg

Table 1. Statewide means (± SD) of field-dressed body weight and number of corpora lutea of harvested female moose in 3 consecutive time periods in New Hampshire, 1988–2009. The only significant differences (P <0.05) occurred in the 1.5 year (yearling) age class (*); all parameters declined from 1988–1998 to 2005–2009.

Age	1988–1998		1999–2004		2005–2009	
	Body weight (kg)					
0.5	110 ± 25	(74)	105 ± 20	(51)	107 ± 22	(45)
1.5	211 ± 31	(175)	203 ± 27	(206)	190 ± 29	(165)*
2.5	258 ± 34	(167)	250 ± 29	(132)	238 ± 31	(117)
3.5	255 ± 35	(102)	246 ± 29	(85)	258 ± 31	(87)
4.5	268 ± 34	(55)	263 ± 35	(68)	247 ± 43	(60)
5.5	261 ± 32	(46)	260 ± 32	(48)	246 ± 29	(40)
≥6.5	258 ± 36	(106)	263 ± 31	(133)	257 ± 36	(131)
	# Corpora lutea					
1.5	0.65 ± 0.65	(187)	0.42 ± 0.52	(200)	0.21 ± 0.42	(169)*
2.5	1.26 ± 0.66	(174)	1.09 ± 0.53	(142)	0.98 ± 0.48	(127)
3.5	1.29 ± 0.62	(102)	1.17 ± 0.60	(90)	1.08 ± 0.54	(91)
4.5	1.53 ± 0.65	(62)	1.26 ± 0.56	(72)	0.98 ± 0.61	(62)
5.5	1.37 ± 0.61	(46)	1.30 ± 0.63	(54)	1.13 ± 0.67	(48)
≥6.5	1.46 ± 0.73	(108)	1.31 ± 0.60	(151)	1.13 ± 0.66	(142)

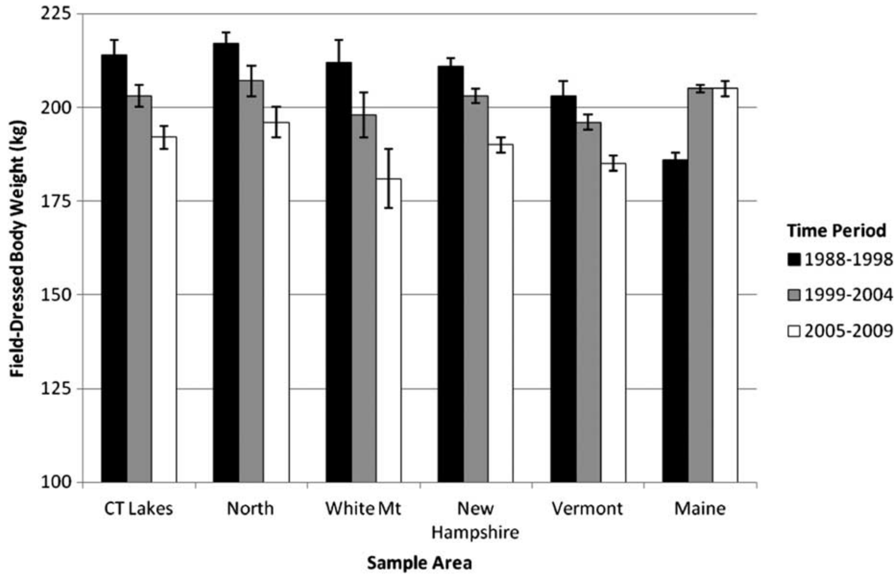

Fig. 2. Mean (± SE) field-dressed body weight (kg) of harvested yearling female moose in 3 sample regions of New Hampshire (1988–2009), and statewide means in New Hampshire, Vermont, and Maine. Body weight declined (P <0.05) in New Hampshire and Vermont from 1988–1998 to 2005–2009; conversely, body weight increased in Maine. For reference, yearlings with body weight <200 kg are considered non-reproductive.

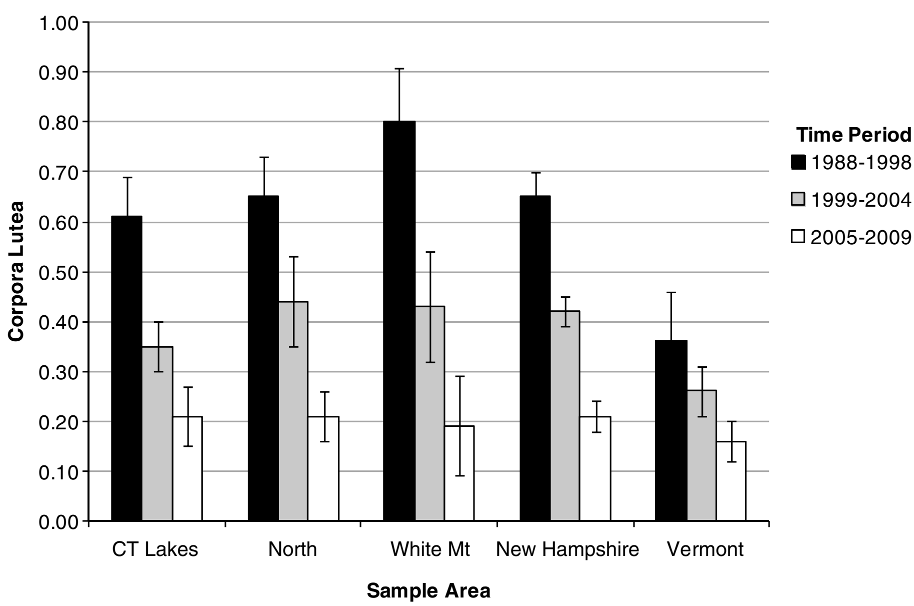

Fig. 3. Mean (± SE) number of corpora lutea (CL) in harvested yearling female moose in 3 sample regions of New Hampshire (1988–2009), and statewide means in New Hampshire and Vermont. Number of CL declined (P <0.05) in New Hampshire from 1988–1998 to 2005–2009; although not different, the decline in Vermont was ~50%.

from 1999–2009. The proportion of yearlings >200 kg in New Hampshire, Vermont, and Maine was 44, 32, and 62%, respectively, in 2005–2009.

Males

Statewide means for body weight, ABD, and antler spread are presented in Table 2. In New Hampshire the only significant differences between time periods in any region occurred in the yearling age class; albeit, all characteristics in Table 2 declined in most age classes in successive periods. Yearling body weight declined 28, 16, and 30 kg from 1988–1998 to 2005–2009 in the CT Lakes (12%, P = 0.000), North (7%, P = 0.011), and White Mountain (14%, P = 0.000) regions, respectively (Table 3). Yearling ABD declined 11% in the CT Lakes (P = 0.023) and 9% in the White Mountains (P = 0.014) regions (Table 3) from 1988–1998 to 2005–2009. Yearling antler spread declined 13, 11, and 15% from 1988–1998 to 2005-2009 in the CT Lakes (P = 0.034), North (P = 0.026), and White Mountains (P = 0.001) regions, respectively (Table 3).

As in New Hampshire, Vermont yearlings declined in each physical characteristic except ABD; body weight declined 9% (P = 0.003) (Table 3) and antler spread 7%

Table 2. Statewide means (± SD) of field-dressed body weight, antler beam diameter (ABD), and antler spread of harvested bull moose in 3 consecutive time periods in New Hampshire, 1988–2009. The only significant differences (P <0.05) occurred in the 1.5 year (yearling) age class (*); all parameters declined from 1988–1998 to 2005–2009.

Age	1988–1998		1999–2004		2005–2009	
	Body weight (kg)					
0.5	119 ± 23	(67)	114 ± 26	(42)	115 ± 25	(46)
1.5	222 ± 39	(377)	206 ± 24	(235)	201 ± 29	(184)*
2.5	271 ± 42	(361)	262 ± 28	(246)	253 ± 30	(219)
3.5	311 ± 36	(229)	294 ± 30	(251)	284 ± 33	(214)
4.5	335 ± 40	(174)	317 ± 32	(172)	312 ± 34	(150)
5.5	350 ± 37	(108)	331 ± 32	(96)	319 ± 37	(93)
≥6.5	352 ± 37	(180)	344 ± 32	(243)	335 ± 36	(218)
	ABD (mm)					
1.5	36 ± 9	(415)	34 ± 7	(262)	34 ± 6	(199)*
2.5	45 ± 7	(391)	44 ± 5	(275)	42 ± 5	(251)
3.5	49 ± 6	(258)	47 ± 5	(291)	46 ± 4	(243)
4.5	54 ± 7	(191)	51 ± 6	(195)	50 ± 6	(162)
5.5	56 ± 8	(124)	54 ± 6	(114)	54 ± 5	(106)
≥6.5	60 ± 6	(214)	59 ± 7	(271)	58 ± 6	(236)
	Antler spread (cm)					
1.5	66 ± 11	(372)	60 ± 12	(247)	59 ± 11	(191)*
2.5	90 ± 11	(363)	85 ± 12	(275)	81 ± 11	(247)
3.5	107 ± 15	(246)	98 ± 14	(289)	96 ± 15	(242)
4.5	120 ± 16	(183)	112 ± 16	(191)	109 ± 16	(157)
5.5	126 ± 16	(114)	121 ± 12	(121)	118 ± 16	(106)
≥6.5	133 ± 15	(197)	131 ± 16	(269)	128 ± 15	(232)

Table 3. Means (± SD) of field-dressed body weight, antler beam diameter (ABD), and antler spread of harvested 1.5 year-old bull moose in 3 consecutive time periods in 3 regions of New Hampshire, 1988–2009. Significant declines (P <0.05) of all parameters occurred in all regions of New Hampshire from 1988–1998 to 2005–2009, except ABD in the North. Body weight and antler spread declined (P <0.05) in Vermont from 1988–1998 to 2005–2009.

	1988–1998		1999–2004		2005–2009	
	Body weight (kg)					
CT Lakes	232 ± 43	(80)	209 ± 26	(44)	204 ± 34	(43)
North	223 ± 30	(119)	212 ± 23	(80)	207 ± 27	(61)
White Mt.	222 ± 44	(102)	194 ± 22	(38)	192 ± 23	(36)
New Hampshire	222 ± 39	(377)	206 ± 25	(235)	201 ± 29	(184)
Vermont	216 ± 27	(58)	202 ± 28	(127)	196 ± 27	(247)
	ABD (mm)					
CT Lakes	38 ± 10	(85)	34 ± 6	(47)	34 ± 6	(47)
North	35 ± 7	(134)	34 ± 7	(99)	34 ± 5	(65)
White Mt.	37 ± 9	(113)	33 ± 7	(44)	34 ± 7	(40)
New Hampshire	36 ± 9	(415)	34 ± 7	(262)	34 ± 6	(199)
Vermont	34 ± 6	(59)	36 ± 6	(128)	34 ± 7	(258)
	Antler spread (cm)					
CT Lakes	68 ± 21	(76)	60 ± 14	(44)	59 ± 10	(44)
North	64 ± 16	(123)	59 ± 12	(96)	57 ± 11	(63)
White Mt.	69 ± 21	(99)	57 ± 11	(40)	59 ± 13	(39)
New Hampshire	66 ± 11	(372)	60 ± 12	(247)	59 ± 11	(191)
Vermont	60 ± 11	(54)	60 ± 12	(118)	56 ± 12	(247)

(P = 0.049) from 1988–1998 to 2005–2009 (Table 3). There was no difference in body weight between 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 ABD was 6% larger in Vermont than New Hampshire in 1999–2004 (P = 0.033).

DISCUSSION

Prior research in New Hampshire (Musante 2006, Musante et al. 2010) indicated that New Hampshire's moose population was effectively stable due to low annual growth rate (estimates = 0.95-1.07). Population stability occurs despite the belief that habitat quality is high (Scarpitti et al. 2005, Scarpitti 2006) and adult productivity and survival are also high (Musante et al. 2010). The population is presumably most influenced by winter ticks that cause periodic, high mortality of calves and reduced productivity in yearling cows (Musante et al. 2010). Our data indicate that body weight and CL count of yearling females have continued to decline through 2005–2009 to about 190 kg and 0.20 CL (Table 1), respectively; ovulation rates of yearlings in North America average 49% (range = 0–100%, Schwartz 2007). Conversely, the ovulation rate of adults was not low in New Hampshire or Vermont (most age classes >90%, Table 1); however, the CL count of adults was in decline in all age classes across the study period (Table 1).

Yearling females <200 kg are considered non-reproductive (Adams and Pekins 1995), and not coincidently, mean body weight of cows with 0 CL was 199 kg in New Hampshire (1988–2009) and 198 kg in Vermont (1993–2009). Productivity from the yearling age class in New Hampshire and Vermont is expectedly low based on ovulation rates ≤20% that are considerably lower (30–50%) than those measured prior to 2000. The mean CL count in New Hampshire (0.22) and Vermont (0.16) was equal to half the proportion of yearlings >200 kg (44 and 32%, respectively); assuming this relationship, the mean CL in Maine is probably >0.30, as 62% of yearlings were >200 kg.

Several factors including habitat quality, weather, and disease/parasites contribute to declining trends in physical parameters of a moose population, the latter 2 typically of short-term impact. 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 4-year study. 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. Although our analysis identified no statistical decline in physical characteristics or ovulation rates of adults, body weight of males and females and age-specific CL counts trended downward across the ~20-year period (Tables 1 and 2).

Calves are most severely impacted by winter tick infestations and some mortality is likely an annual event; however, even surviving calves presumably experience lower body weight and reduced fecundity as yearlings (Samuel 2004, 2007, Musante et al. 2010). The declining trend in yearling condition in New Hampshire and Vermont from 1988–2009 suggests that average tick loads might impact moose populations through reduced fitness and 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 in New Hampshire in 1988–1998 (217 kg, Fig. 2). As a region, it is evident that productivity of yearling cows is low with CL counts probably <40% even in Maine based on comparative data from New Hampshire and Vermont (Fig. 2 and 3).

New Hampshire's moose population was still expanding in 1988–1998, and their physical characteristics may have peaked during this period of high resource availability related to extensive forest harvesting in the 1980s (see Bontaites and Gustafson 1993). Their gradual decline since 1988 may reflect the combined influences of saturation of available habitat, reduced availability of preferred habitat, and gradual decline in habitat quality due to subsequent forest maturation. Further, concern exists about forest regeneration in the face of dense populations in northern areas of all 3 states, and isolated examples exist (see Bergeron et al. 2011); that these populations may express self-limiting impacts on habitat quality, hence fecundity, is possible. However, the steep decline in yearling body weight and that the yearling ovulation rate is well below the North American average suggests that other contributing factors exist, particularly given the relative stability of measurements in adult moose.

In fact, winter ticks cause age-specific impacts because calves have higher, relative tick numbers than adults, and severe hair-loss is evident on calves even in low/average tick years (Samuel and Barker 1979, Samuel 2004, Sine et al. 2009, Bergeron 2011). The lack of a local epizootic of winter tick since 2002 and the declining trend in yearling physical characteristics supports the hypothesis that annual winter tick numbers affect population dynamics through reduced growth and fecundity of yearling moose (i.e., surviving calves). Recent warmer and shorter winters that maximize spring survival and autumn questing of winter ticks presumably enhance this relationship by causing an increase in annual tick numbers, and likely increase the probability of an epizootic that produces substantial calf mortality; anecdotal reports from all 3 states suggest that a local epizootic in combination with deep snow caused high calf and yearling mortality in winter 2010–2011. The relative influences of habitat, population density, weather, and parasites on the population dynamics of moose is difficult to ascertain, and likely varies temporally. Collection of long-term data sets of tick numbers and physical parameters of harvested moose in concert with annual, spring hair-loss surveys would better document the relationships between winter tick and population dynamics of moose in New Hampshire.

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