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TRENDS OF WINTER NUTRITIONAL RESTRICTION, TICKS, AND NUMBERS OF MOOSE ON ISLE ROYALE

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Abstract: During a 7-year study, we monitored winter nutritional restriction of moose (*Alces alces*) and moose numbers on Isle Royale (winters 1987–88 to 1993–94). Over the 7 winters, the estimated moose population decreased 26% from an historic high of 1,653 (winter 1987–88) to 1,216 (1989–90), then increased to a new high (1,880 and 1,770) by winters 1992–93 and 1993–94. During that time, there was a significant ($P = 0.0486$) negative relation ($r = -0.84$) between the percent of urine specimens collected from snow (snow-urine) in late winter with urea nitrogen:creatinine (UN:C) ratios ≥ 3.5 mg:mg and percent change in the moose population from winter 1987–88. Mean urinary UN:C of moose residing on the east and west ends of Isle Royale declined ($P \leq 0.0001$) among years; however, slopes of the 2 trends were different ($P = 0.0001$). The nutritional restriction and decline in moose numbers appeared to involve an epizootic of the winter tick (*Dermacentor albipictus*; indicated by percent moose observed with tick-induced hair breakage and loss). During winters 1987–88 to 1989–90, the percentage of late winter snow-urine specimens with UN:C ratios indicative of severe nutritional restriction ranged from 47 to 58%; however, the percentage decreased to zero by winter 1993–94 as the tick infestation subsided and moose numbers increased.

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Key words: *Alces alces*, condition indices, *Dermacentor albipictus*, Isle Royale, moose, nutritional restriction, urea nitrogen, urine chemistries, winter ticks.

Like other northern cervids, moose exhibit seasonal variations of dry matter intake, body mass, metabolic rates, and energy requirements with pronounced reductions occurring during winter (Schwartz et al. 1984, 1987, 1988; Regelin et al. 1985; Renecker and Hudson 1985, 1989). Generally, this winter nutritional challenge is a response to coincident decreased forage availability and quality (Krefting 1951, Cumming 1987, Risenhoover 1987) and increased energetic costs of movement (Telfer and Kelsall 1984). However, severity of nutritional restriction may be mediated by a variety of environmental factors, e.g., species composition of available forage, winter weather conditions, moose density, and disease.

There are a number of advantages inherent in multi-year studies of wildlife populations in a given location. The primary advantage is that with the passage of time, there is an increasing probability of occurrence of natural, marked environmental perturbations that might induce unique responses in populations, thus affording the opportunity to study complex relations between populations and temporally varying environmental factors. Findings from such research may generate important hypotheses concerning ecological relations.

Previously, we reported urinary UN:C ratios of moose in Isle Royale National Park experiencing severe nutritional restriction during winters 1987–88 and 1988–89 (DelGiudice et al. 1991a). These data indicated that nutritional restriction in moose was more severe on the east end of the island than on the west end. During winter 1987–88, moose numbers were estimated to be at an historic high, but there was evidence of the beginning of a winter tick epizootic (Peterson 1988). By 1989, moose numbers had decreased 16%, and severe nutritional restriction was still evident in a high proportion of sampled moose. We continued to monitor winter nutritional restriction of moose on the west and east ends of Isle Royale and moose numbers island-wide. Herein, we report and discuss 7-year trends and interactions of winter nutritional restriction, ticks, and moose numbers on Isle Royale.

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Park and individuals for field assistance and K. D. Kerr, M. D. Lewis, and S. K. Ruen for technical support in the laboratory. We appreciate the statistical consultation and manuscript review of M. R. Riggs.

STUDY AREA

Isle Royale, 544 km² in area, 72 km long and 14 km at its widest point (Peterson 1977), is located at 47°55'N, 89°W and about 24 km south of the Canadian border. Elevations on Isle Royale range from 181 to 419 m (Peterson 1977). The island consisted primarily of a bedrock strata. The east end of the island was characterized by thin, azonal soils, abundant bare rock ridges, and boreal forest of balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*; Krefting et al. 1970, Peterson 1977). There were associated stands of white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). In contrast, soils on the west end were thicker, more developed, contained abundant glacial debris, and may exhibit a higher nitrogen content in the absence of moose browsing (Huber 1973, Peterson 1977, Pastor et al. 1988). Balsam fir occurred on the west end, but at lower densities than on the east end (Brandner et al. 1990; B. E. McLaren, unpubl. data). More apparent on the west end are mixed northern hardwood stands of sugar maple (*Acer saccharum*), yellow birch (*B. allegheniensis*), trembling aspen, and white birch. Northern white cedar (*Thuja occidentalis*) and white spruce also were present. More detailed descriptions of Isle Royale may be found elsewhere (Krefting et al. 1970, Huber 1973, Krefting 1974, Peterson 1977, Risenhoover and Peterson 1986, Pastor et al. 1988).

Snow depth was similar on both ends of the island. Daily snow depths, January–early March 1988–93, were 34–50, 63–81, 45–69, 38–53, 38–63, and 37–55 cm. During January–late February 1994, snow depths were 28–60 cm (Isle Royale Natl. Park records, Houghton, Mich.). During December–March, ranges of mean monthly ambient temperatures were –16 to –4.8, –16 to –9.4, –17.9 to –3.9, –17.2 to –5.1, –11.3 to –5.5, –14.1 to –5.1, and –22 to –3.1 C for 1987–88 to 1993–94 (Environ. Can., Thunder Bay, Ont. 1987–1994).

About 15 additional species of mammals occur on Isle Royale, including the gray wolf (*Canis lupus*), red fox (*Vulpes vulpes*), snowshoe hare (*Lepus americanus*), and beaver (*Castor*

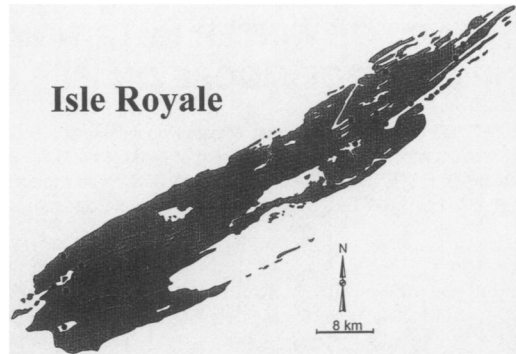


Fig. 1. Locations of sites where moose urine specimens in snow (snow-urine) were collected for physiological assessment of nutritional restriction, Isle Royale, winters 1987–88 to 1993–94.

canadensis). Predation by wolves continues to be the primary proximate cause of death for moose of Isle Royale (Peterson 1977, 1994).

METHODS

Moose Snow-Urine Sampling

We collected specimens of moose snow-urine during mid- (14 Jan–15 Feb) and late winters (22 Feb–2 Mar) 1988–94 on the west and east ends of Isle Royale as described in DelGiudice et al. (1991a). Specific locations included Windigo, Feldtman, and Grace Creek on the west end, and Tobin, Benson, and Daisy Farm on the east end (Fig. 1). Sampling areas ranged in size from 2 to 4 km².

To ensure collection of fresh specimens of urine, and thus allow association of urinary data with specific times during winter, samples were collected within 24–48 hours of a recent snowfall. We employed a haphazard sampling design, in which personnel traversed areas known to have moose until they intersected moose tracks, whereupon, the trail was followed until a sample was found. Specimens were collected and handled as described by DelGiudice et al. (1991a). To avoid multiple samples from the same moose during a collection, collectors were selective with respect to the sets of tracks they followed, and they minimized the number of specimens they obtained along a specific trail relative to the number of moose being tracked (DelGiudice et al. 1991a). Track size was used to discriminate among individual moose (e.g., calves from moose >1 yr old). Samples from calves were generally avoided.

Moose Counts and Winter Tick Assessments

Moose were counted from fixed-wing aircraft once each winter between late January and late February. Each year identical small plots (averaged 1 km²) totalling 15 to 20% of the island area (544 km²) were surveyed intensively by circling overhead (mean search intensity 14 min/km²). Sampling intensity was similar on the east and west ends of the island. Plots were established randomly within each of 3–4 strata of relative density. Stratum boundaries were redrawn each year based on systematic (every 3 km) transects flown to assess relative track density 2–4 days after fresh snow, but in practice, there is minimal change in strata boundaries because we counted moose after their distribution had stabilized in mixed or conifer-dominated habitats. The plots were partitioned into 3–4 strata to reduce variance in the final estimate that is calculated (with 90% confidence limits) according to Gasaway et al. (1986). A 75% sightability factor, derived from tests with radiocollared moose, was employed to correct the estimates (Peterson and Page 1993). While the east and west ends have vegetation differences, once the distribution of moose has stabilized, their selection of habitat was similar throughout the island.

Assessment of winter tick infestation was done by recording tick-induced hair damage during aerial surveys of moose, 1988–94. The assessment was based on the proportion of moose on census plots that had patterns of hair breakage and loss (i.e., alopecia) typical of that induced by winter ticks (McLaughlin and Addison 1986, Samuel et al. 1986, Samuel 1991). There are no other known causes of this type of hair loss on moose in North America (Samuel 1989). Observations of tick-induced hair damage and loss were first made in winter 1987–88, but data recording was casual. We rigorously began recording observations during winter 1988–89. Because tick-induced hair loss is minimal in January and February (Samuel and Welch 1991), when aerial surveys were done, observations made then might underestimate the extent of the epizootic.

Hides of 2 moose, a female calf and an adult cow, found dead in February and early March on Isle Royale, were shipped frozen to the University of Alberta. About 7,500 and 14,000 cm² of hide were examined for winter ticks following

the digestion technique of Welch and Samuel (1989).

Laboratory and Statistical Analyses

We chemically analyzed urinary urea nitrogen (UN), creatinine (C), and potassium (K) as described in DelGiudice et al. (1990). Urea nitrogen and K data were compared as ratios to C to correct for differences in hydration, body size, and dilution by snow (DelGiudice et al. 1988, 1991a). Potassium:creatinine ratios were multiplied by 1,000 for ease of comparison within this study and with data reported elsewhere (DelGiudice et al. 1991a, DelGiudice 1992). Creatinine ratios of several urinary chemistries diluted in snow accurately represent these ratios in bladder urine (DelGiudice et al. 1988, White et al. 1995).

Statistical analyses included urinary data from DelGiudice et al. (1991a) to permit a more complete examination of multi-year trends. Different from DelGiudice et al. (1991a), data collected during early February 1988 and 1989 were reclassified as mid-winter to facilitate consistency with winters 1990 through 1994. Urinary UN:C and K:C ratio data were analyzed by 3-way analysis of variance (ANOVA) with year (1988–94), location (east vs. west end of island), and season (mid- and late winter) as main effects. Although year was treated as a categorical effect in the ANOVA model, orthogonal polynomial contrasts were included in the analysis to test for the alternative of a trend across years at each location (Montgomery 1991:118–120). Before analyses, UN:C and K:C ratios were log-transformed. All significant ($P \leq 0.05$) interactions were examined graphically to determine which ones were of biological consequence (Neter et al. 1990:681–608, 821–826). Linear regression analyses were employed to examine relations of moose population change with UN:C and effects of snow depth and Julian day on UN:C ratios. All analyses were made with the SAS system (SAS Inst. Inc. 1988). Significant differences in moose estimates were indicated if upper and lower 90% confidence limits from annual counts did not overlap.

RESULTS

Moose with hair damage and loss caused by winter ticks were first observed in February 1988, but such evidence was most prevalent in February 1989 (Fig. 2). Numbers of winter ticks on the collected hides of a calf and a cow were

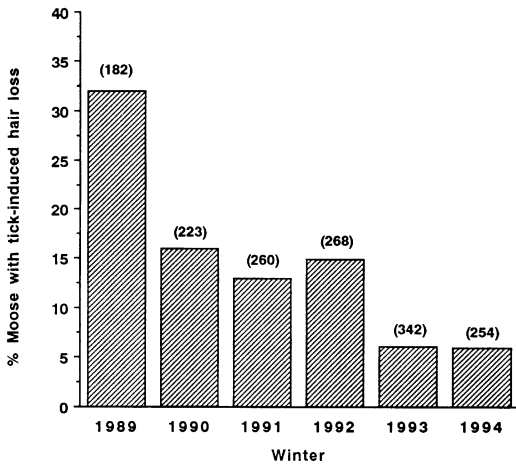


Fig. 2. Percent moose at Isle Royale observed during aerial census with hair damage and loss caused by winter ticks (*Dermacentor albipictus*), Isle Royale, winters 1988–89 to 1993–94. (no. in parentheses are total moose observed.)

estimated at 28,338 (1.89 ticks/cm²) and 23,590 (0.85 ticks/cm²). Prevalence decreased in 1990, but was still 16% (Fig. 2). Annual prevalences were low in winters 1993 and 1994.

The moose population declined ($P \leq 0.10$) 26% from 1988 to 1990, then increased ($P \leq 0.10$) steadily (55%) until 1993 (Fig. 3). Moose numbers remained stable through 1994. Based on classification of all moose counted on plots (n in Fig. 2) during 1988–94, calves composed 15, 13, 15, 14, 11, 14, and 12%.

There was no significant ($F = 1.40$; 6, 358 df; $P = 0.21$) year \times location \times season interaction for mean urinary UN:C. The year \times location interaction was highly significant ($F = 5.82$; 6, 358 df; $P < 0.001$; Fig. 4). The year \times season ($F = 2.09$; 6, 358 df; $P = 0.054$) and location \times season ($F = 4.05$; 1, 358 df; $P = 0.045$) interactions were marginally significant, and after graphical examination, deemed of little biological consequence. From 1988 to 1994, mean urinary UN:C declined significantly for both east (–75%; $F = 158.63$; 1, 358 df; $P < 0.001$) and west-end (–36%; $F = 36.54$; 1, 358 df; $P < 0.001$) moose. However, the slopes of their trends were different ($F = 25.53$; 1, 358 df; $P < 0.001$; Fig. 4); it was steeper in east-end moose during the first 4 years. Mean UN:C ratios were affected by year ($F = 33.50$; 6, 358 df; $P < 0.001$) and location ($F = 117.40$; 1, 358 df; $P \leq 0.001$), but not by season ($F = 0.22$; 1, 358 df; $P = 0.64$).

During late winters 1988–90, 47.4–57.9% of

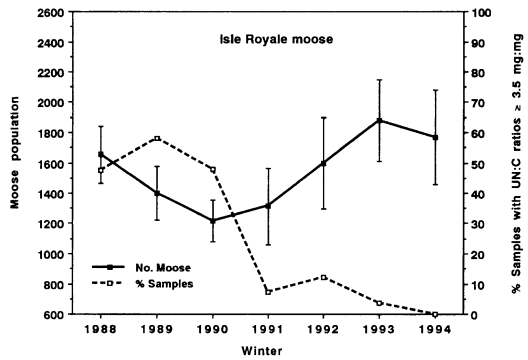


Fig. 3. Estimates of the number of moose ($\pm 90\%$ confidence limits) and percentage of moose urines voided in snow during late winter with urea nitrogen : creatinine ratios indicative of severe nutritional restriction, Isle Royale (east and west ends pooled), winters 1987–88 to 1993–94. (sample sizes were 19–28, and data from 1988 and 1989 were recalculated from DelGiudice et al. 1991a.)

moose sampled on the east and west ends of Isle Royale (island-wide) exhibited UN:C ratios (≥ 3.5 mg:mg) indicative of severe dietary energy restriction and accelerated net catabolism of protein (Fig. 3). This percentage declined steadily to 0% by 1994 (Fig. 3). Over the 7-year study period, we found a significant ($F = 11.70$; 1, 5 df; $P = 0.019$) negative linear relation ($r = -0.84$) between the percent change in moose numbers from winter 1988 and the percentage of snow-urine samples from the previous late winter with UN:C ratios indicative of severe dietary energy restriction (≥ 3.5 mg:mg; Fig. 5). During mid- and late winters 1988–90, the percentage of sampled moose with UN:C ratios indicative of severe dietary energy restriction was greater on the east end of the island (Fig. 6).

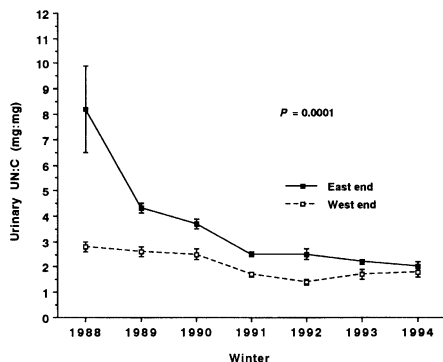


Fig. 4. Mean (\pm SE) urea nitrogen : creatinine ratios of urine voided in snow by moose on the west and east ends of Isle Royale, winters 1987–88 to 1993–94. (sample sizes were 22–35, and data from 1988 and 1989 were recalculated from DelGiudice et al. 1991a.)

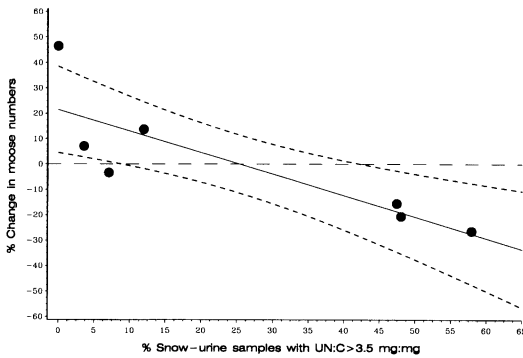


Fig. 5. The relation between the percentage of late winter snow-urine samples with urea nitrogen:creatinine (UN:C) ratios indicative of severe nutritional restriction and the percent change in the following winter's moose numbers from winter 1987-88 ($y = 21.495 - 0.847x$, $r^2 = 0.70$, $P = 0.019$), Isle Royale, winters 1987-88 to 1994-95. Dotted lines represent 90% confidence limits.

The disparity remained evident until late winter 1994. We detected no relation between snow depth and UN:C during the study.

The year \times location \times season interaction was nonsignificant ($F = 1.40$; 6, 357 df; $P = 0.22$) for mean K:C ratios. There was a marginally significant ($F = 2.20$; 6, 357 df; $P = 0.043$) year \times location interaction (Fig. 7); location \times season was highly significant ($F = 10.23$; 1, 357 df; $P = 0.002$), but the trends were limited to just 2 points (mid- and late winter). Mean K:C remained relatively stable from early to late winter in moose residing on the east end of Isle Royale, but declined in west end moose. The year \times season interaction was not significant ($F = 0.72$; 6, 357 df; $P = 0.64$). Year was the only significant ($F = 11.84$; 6, 357 df; $P < 0.001$) main effect for K:C.

DISCUSSION

Given the seasonal dynamics of weather and availability and quality of forage, winter nutritional restriction and condition deterioration in moose are expected (Hjeljord et al. 1982; Schwartz et al. 1984, 1987, 1988; Regelin et al. 1985; Renecker and Hudson 1985, 1989). However, mid- and late winter UN:C data from Isle Royale moose indicated abnormally severe nutritional (i.e., dietary) restriction in a high proportion of moose from 1988 to 1990. Coincident with a 26% decline in the population during this period, high proportions of late winter snow-urine samples (47-58%), collected primarily from moose >1 year old, exhibited UN:C ratios indicative of accelerated endogenous

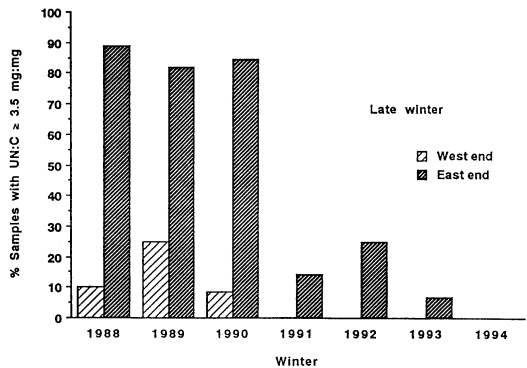
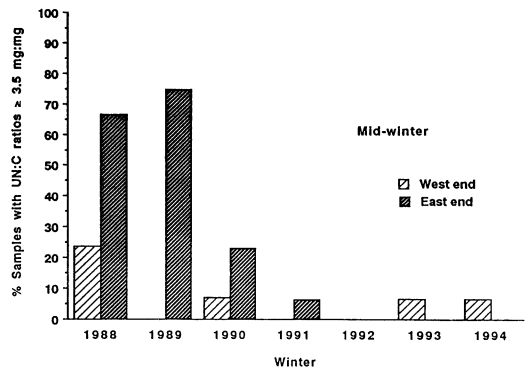


Fig. 6. Percentage of urine specimens voided in snow by moose exhibiting urea nitrogen:creatinine ratios indicative of severe nutritional restriction, east and west ends of Isle Royale, during mid- and late winters 1987-88 to 1993-94. (sample sizes were 8-21, and data from 1988 and 1989 were recalculated from DelGiudice et al. 1991a).

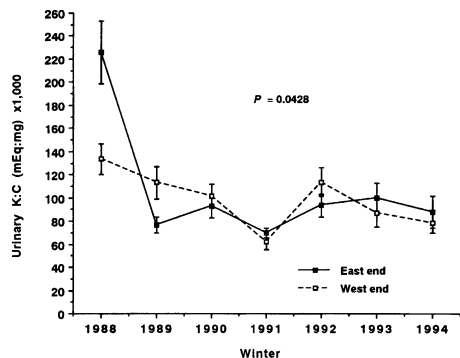


Fig. 7. Mean (\pm SE) potassium:creatinine ratios of urine voided in snow by moose on the west and east ends of Isle Royale, winters 1987-88 to 1993-94. (sample sizes were 22-35, and data from 1988 and 1989 were recalculated from DelGiudice et al. 1991a).

protein catabolism (≥ 3.5 mg:mg; Hundertmark et al. 1990; DelGiudice et al. 1991a,b, 1994).

To illustrate the biological significance of elevated UN:C ratios relative to condition deterioration, consider the difference (2.5 mg:mg) in late winter mean UN:C ratios of east end moose between winters 1988–89 (4.3 mg:mg) and 1993–94 (1.8 mg:mg) when assessed nutritional restriction was severe and mild. Assuming the difference of 2.5 mg urea N excreted/mg creatinine is derived from endogenous protein catabolism, a loss of 62.5 mg lean body mass (LBM)/mg creatinine is indicated (Kinney et al. 1970, Runcie and Hilditch 1974). Employing creatinine coefficients in the range of 19–31 mg/kg/day (Cool 1992), this would represent a LBM loss of 0.5–0.8 kg/day for a 400-kg moose. Although we have no data to indicate the duration of such a catabolic rate during winter 1988–89, our data reflect a serious rate of deterioration in body condition.

Initial evidence of the winter tick epizootic, loss of hair by infested moose during February 1988, was the direct result of vigorous grooming (e.g., licking, biting, rubbing, and scratching with the hind feet), which begins in January and becomes most intense in March and April (Samuel 1991). Uninfested moose rarely groom during this period (Samuel 1991). Potential adverse consequences of grooming and hair loss relative to activity budgets, hypothermia, reduced fat stores, and compromised immunity have been discussed elsewhere (McLaughlin and Addison 1986, Glines and Samuel 1989, Welch et al. 1990, Samuel 1991).

The interaction between nutritional state of the individual and tick infestation is complex. Generally, animals on a lower plane of nutrition carry more ticks (Gladney et al. 1973) and exhibit more serious clinical manifestations (e.g., anemia and other physiologic effects) as a consequence (O'Kelly and Seifert 1970, Glines and Samuel 1989). For free-ranging moose, nymphal and adult ticks engorge on blood during the critical March–April period of progressive nutritional and energetic stress, then drop off (Glines and Samuel 1989).

The high proportion of moose on Isle Royale with tick-induced hair damage and loss during winter 1988–89 (Fig. 2) indicated that the tick epizootic was most severe during that year (Samuel 1991, Samuel and Welch 1991; W. M. Samuel, unpubl. data). Ticks and hair damage were prominent on all carcasses found where

hide remained. During the same winter, a high prevalence of hair loss and/or significant mortality of moose attributable to winter ticks also was recorded in Elk Island National Park, Alberta (W. M. Samuel, unpubl. data), Algonquin Park, Ontario (Wilton and Garner 1993), Manitoba (V. Crichton, pers. commun.), and Minnesota (W. Peterson, pers. commun.). During this study, moose density on Isle Royale ranged from 2.2 to 3.5 moose/km², numbers that exceeded densities of the previous 3 decades (McLaren and Peterson 1994). The population trend we observed appeared to be largely a function of mortality rate, as recruitment was relatively stable (calves composed 11–15% of the moose observed during the annual aerial counts). During at least 12 winters since 1930, winter tick epizootics have been associated with major die-offs of moose in central Alberta (Webb 1959, Samuel and Barker 1979, C. B. Blyth and R. J. Hudson, unpubl. data).

Tick-related mortality of moose in many areas of North America in 1989 suggests a common extrinsic influence, perhaps independent of moose density on Isle Royale. Late March to late April is the time when blood-engorged, adult female winter ticks drop from moose (Drew and Samuel 1989). Low precipitation and warm temperatures during April appear to be conducive to maximum survival and subsequent reproduction of ticks, thus potentially resulting in increased numbers of ticks the following autumn–winter. Specifically, snow cover adversely affects survival of disengaging females (Drew and Samuel 1986), and Wilton and Garner (1993) have suggested that survival of winter ticks decreases at mean April temperatures < 3 – 4 C. Precipitation during April 1987, 1988, and 1989 was unusually low (≤ 11 cm) compared to 1990–94 (75, 29, 46, 55, and 48 cm; Natl. Oceanic and Atmos. Adm. 1987–94). In 1987, snow cover (2.5 cm) occurred no later than 2 April, and no snow cover was recorded for April 1988 (Natl. Oceanic and Atmos. Adm. 1987, 1988). During April 1989, following the winter of peak infestation, a snow depth of 12.5 cm was recorded as late as 20 April (Natl. Oceanic and Atmos. Adm. 1989). Mean temperature was elevated during April 1988 (3.8 C) and 1991 (4.8 C) compared to April 1989, 1992–94 (all ≤ 1.6 C), and 1990 (2.9 C) (Environ. Can., Thunder Bay, Ont. 1988–94).

From 1991 to 1994, both mean UN:C and proportions of snow-urine samples with UN:C

ratios ≥ 3.5 mg:mg declined, thus, indicating a moderating of winter nutritional restriction (DelGiudice et al. 1991a,b). Coincidentally, population density exhibited an upward trend. A significant negative correlation between population rate-of-increase (% change from winter 1988) and UN:C ratios suggests that severe nutritional restriction associated with the tick infestation may have contributed to the decline in moose density on Isle Royale during 1988–90. Data for the 1988–94 period are consistent with a continuous linear rate of change, but because of an absence of data, we cannot rule out the possibility of a single step decline in moose numbers between 13 and 48% on the x-axis (Fig. 5).

Interestingly, during 1988–92, when winter ticks were most prevalent, UN:C ratios indicated that late winter nutritional restriction was more severe for moose at the east end of Isle Royale compared to the west end. However, during late winters 1993 and 1994, the east-west difference in restriction was almost non-existent. Density-independence of these spatial differences and temporal changes is indicated by absence of a difference in moose densities between the east and west sides of the island throughout the 7-year study and by moderation of the apparent nutritional restriction as the tick infestation subsided and moose numbers increased from 1991 to 1994. Uncertainty arising from ecological complexity and inevitable shortcomings in available data render this finding difficult to explain. However, a marked difference in east versus west habitat composition may be an important factor. The west end of the island comprises a diversity of forest types, whereas the east end is characterized by a greater density of balsam fir (Krefting 1974, Brandner et al. 1990, McLaren and Peterson 1994). These habitat differences have been associated with differences in diets of the moose (Krefting 1974). Additional research is warranted to examine more closely the interrelations of dietary differences, nutritional restriction, and the stress imposed by winter tick infestation.

Ours was an observational study with inferences drawn from correlational data. Nevertheless, it demonstrated that population density for moose per se had little association with either the population rate-of-increase or nutritional status. These findings were consistent with the conclusion of McLaren and Peterson (1994) that Isle Royale moose were released from

top-down control by wolf predation during the 1980s after a wolf decline that was linked circumstantially to a new disease. We predict that Isle Royale moose, lacking regulation by wolves or a density-dependent reduction in recruitment, will continue to increase until other sources of mortality intervene. Further, UN:C data suggest the existence of a detectable ecological linkage between nutritional restriction of Isle Royale moose and population performance.

From our findings and those of other pertinent studies on Isle Royale, we submit the following 2 hypotheses for future research. First, we hypothesize that a large part of the stress imposed by winter tick infestation on moose is mediated through its effect on nutritional restriction, with the greatest effect on moose that rely heavily on balsam fir (i.e., implication of restrictive effects of secondary compounds). A corollary to this hypothesis is that the nutritional restriction is related directly to preoccupation of infested moose with grooming. Second, we hypothesize that effects of winter ticks on moose across geographic regions are primarily weather-dependent and density-independent.

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MORTALITY PATTERNS OF WHITE-TAILED DEER IN MICHIGAN'S UPPER PENINSULA

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Abstract: We radiotracked 95 white-tailed deer (*Odocoileus virginianus*, all age classes) in Michigan's Upper Peninsula between January 1992 and January 1995 for a total of 38,888 deer-days. Fifty-eight deer died: 12 due to predation, 6 due to malnutrition, 14 due to other or unknown sources, and 26 killed by hunters (including 1 that was poached). Analysis of mortality indicated rates of annual nonhunting mortality were 0.19 (SE = 0.09) for adult females, 0.00 (SE = 0.05) for adult males and yearling females, and 0.16 (SE = 0.07) for yearling males. Hunting mortality was 0.04 (SE = 0.10) for adult females, 0.72 (SE = 0.12) for adult males, 0.12 (SE = 0.09) for yearling females, and 0.47 (SE = 0.10) for yearling males. Hunting mortality was higher among males in both age classes ($P < 0.01$) though nonhunting mortality was equivalent ($P \geq 0.05$). Seasonal mortality rates of males and females differed during the fall ($P < 0.001$), coincident with Michigan's hunting seasons. Hunting mortality was significantly higher for yearling and adult males due to hunting regulations that limited harvest of antlerless deer; consequently, adult sex ratios were skewed towards females.

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A major difficulty in the analysis of wildlife population dynamics lies in obtaining useful estimates of survival (Eberhardt 1985), and these estimates are rare in vertebrate literature (Gaillard et al. 1993). The challenge for managers and researchers is that much of the available data on survival depends on uncertain inference

based on age-structure data (Caughley 1977, McCullough 1979, Eberhardt 1985).

In ungulates, rates of nonhunting mortality commonly are higher for males due in part to the physiological demands of larger body size and behaviors related to the establishment of male dominance patterns during the breeding season (Clutton-Brock et al. 1982, Gaillard et al. 1993, Owen-Smith 1993). Hunting mortality frequently is higher among males as well due to hunter preference for male traits (larger horns, antlers, larger body size) and regulations that restrict harvest of females (Dusek et al. 1989, Nixon et al. 1991). Depending on the degree to

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