



CLIMATE CHANGE, WINTER NUTRITIONAL RESTRICTION, AND THE DECLINE OF MOOSE IN NORTHEASTERN MINNESOTA, WINTERS 2013–2017

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SUMMARY OF FINDINGS

The moose (*Alces alces*) population in northeastern Minnesota has declined an estimated 58% from 2006 to 2017. As in northwestern Minnesota, a number of complex ecological relationships between undernutrition, pathogens, predation, and environmental factors (e.g., habitat, temperature) are likely exerting pressure on moose and contributing to this recent decline. Nutrition is centrally related to our understanding of all other aspects of wildlife ecology, including population performance. Winter nutritional restriction of moose and other northern ungulates may be physiologically assessed by serial collection and chemical analysis of fresh urine in snow (snow-urine); urea nitrogen:creatinine (UN:C) ratios have shown the greatest potential as a metric of winter nutritional status with values <3.0, 3.0–3.4, and ≥ 3.5 mg:mg being indicative of moderate (normal), moderately severe, and severe nutritional restriction, respectively. During 6 January–28 March 2013–2017, we collected annual totals of 123, 307, 165, 189, 160 moose snow-urine samples, and mean seasonal UN:C ratios were 3.7, 2.9, 2.9, 3.5, and 3.7 mg:mg for the 5 winters, respectively. The mean population UN:C ratios for winters 2013, 2016, and 2017 were above the threshold indicative of severe nutritional restriction (i.e., a starvation diet) and accelerated body protein catabolism. During 2014 and 2015 the corresponding values reflected moderate nutritional restriction. Most indicative of the unique severity of nutritional restriction in 2013, nearly one-third of all samples collected yielded UN:C ratios ≥ 3.5 mg:mg.

Perhaps the ultimate value to management of nutritional assessments of free-ranging animals comes when the findings can be related to the performance and dynamics of the population and other ecological factors challenging that performance. Presently, our population-level nutritional assessments are closely tracking population estimates ($r^2 = 0.75$) and calf production ($r^2 = 0.85$) of moose in northeastern Minnesota. Although nutritional restriction varied among the 5 winters, elevated UN:C values suggested a level of deprivation not supportive of population stability or growth. Climate change, reflected by the heat stress index for moose, and variation in winter conditions, as indexed by the winter severity index (WSI), were not related to nutritional restriction of moose. For the 5 winters, we also have documented that the level of severe nutritional restriction is inversely related ($r = -0.86$) to variation of *natural* winter survival of global positioning system (GPS)-collared adult moose. While these relationships do not substantiate cause-and-effect, presently it provides the best preliminary empirical evidence that inadequate winter nutrition at the population level is intricately related to the declining trajectory of moose numbers in northeastern Minnesota.

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INTRODUCTION

Declines in regional populations of moose (*Alces alces*) along the southern periphery of their global range have been common in recent decades (Timmerman and Rodgers 2017). In northeastern Minnesota the estimated 2017 population (3,710 moose) is 58% less than in 2006 (8,840 moose, DelGiudice 2017), exhibiting a trajectory similar to that documented previously for moose in northwestern Minnesota, where the population decreased from ~4,000 in the mid-1980s to <100 moose in 2007 (Murray et al. 2006). Furthermore, mean annual mortality rates of collared adult moose were similarly high (21%) in the northwest and northeast during the declines (Murray et al. 2006; Lenarz et al. 2009; R. A. Moen, unpublished data). In northwestern Minnesota, malnutrition and pathogens were identified as important factors influencing the population's decreasing trajectory (Murray et al. 2006). In northeastern Minnesota a recent (2013–2016) aggressive study of global positioning system (GPS)-collared, adult moose reported a mean annual mortality rate of 15.3%, with health-related factors (e.g., parasites, disease) accounting for about two-thirds of the deaths, wolf (*Canis lupus*) predation for one-third, and complex interactions between the 2 categories well-documented (Carstensen et al. 2017). In the earlier studies, climate change (i.e., warming temperatures) was implicated in both population declines (Murray et al. 2006; Lenarz et al. 2009, 2010).

These temperature-survival relationships are complex, and indicate that climate change can directly and indirectly impact ungulate populations (Bastille-Rousseau et al. 2015, Davis et al. 2016, Street et al. 2016). Moose are particularly well-adapted to cold climates, but temperatures that exceed “heat stress” thresholds of 14 to 24°C during summer and –5°C during winter may increase metabolic rates, induce energy deficits, and hasten deterioration of body condition (Renecker and Hudson 1986, 1990; Broders et al. 2012; McCann et al. 2013). These thresholds may be influenced by exposure to solar radiation and wind (Renecker and Hudson 1990, McCann et al. 2013). Nutritional and health status (e.g., disease, parasites), behavioral responses (e.g., altering movement, foraging, and bedding patterns), and quality of available habitat have the potential to affect the animal's ability to mitigate negative impacts from heat stress (Van Beest et al. 2012, Street et al. 2016).

Energy balance is central to animal fitness, which is critical to survival and reproduction, the 2 drivers of population performance (Robbins 1993). The natural “nutritional bottleneck” of winter typically imposes the greatest challenge to the supply side of energy budgets of moose and other northern ungulates (Mautz 1978, Schwartz and Renecker 2007). Gestation at this time increases energetic and nutritional demands, particularly during late-winter and early-spring (Robbins 1993). Although moose are generally well-adapted to this seasonal nutritional deprivation, elevated ambient temperatures exceeding heat stress thresholds, coupled with the influence of other compromising extrinsic factors (e.g., pathogens, poor quality forage and low availability of thermal cover, densities of conspecifics or other nutritionally competing species) can exacerbate energy deficits and associated consequences for adult and juvenile survival, subsequent reproductive success, and population dynamics (Robbins 1993; DelGiudice et al. 1997, 2001).

Winter nutritional restriction of moose and other northern ungulates can be physiologically assessed at the population level by serial collection and chemical analysis of fresh urine voided in snow (snow-urine; DelGiudice et al. 1988, 1997, 2001; Moen and DelGiudice 1997, Ditchkoff and Servello 2002). Urea nitrogen (interpreted as a ratio to creatinine, UN:C), the end-product of protein metabolism, is one of many chemistries investigated for its value as a physiological metric of the severity of nutritional restriction (DelGiudice et al. 1991a,b, 1994). In healthy moose, urinary UN:C values decrease (N conservation) in response to diminishing intake of crude protein and digestible energy, but as dietary restriction and negative energy balance become more severe

and fat reserves are depleted, ratios increase to notably elevated values in response to accelerated net catabolism of endogenous protein. Snow-urine UN:C ratios exhibited differential effects of a winter tick (*Dermacentor albipictus*) epizootic and habitat differences on the severity of nutritional restriction of moose on Isle Royale, and were strongly related to dynamics of the population, including a pronounced decline and recovery to historically high numbers (DelGiudice et al. 1997).

OBJECTIVES

1. To determine how nutritional restriction varies annually and as winters progress
2. To examine potential relationships between the severity of nutritional restriction and the winter heat stress index (HSI) for moose, seasonal survival rates of GPS-collared adult moose, and annual population estimates of moose

We hypothesized that increasing winter ambient temperatures, exceeding the HSI threshold, are contributing to the severity of nutritional restriction and energy deficit of moose, decreases in survival by various proximate factors, and diminishing performance of the population. Findings will set the stage for additional work assessing nutritional relationships of moose to variations in habitat and other factors.

STUDY AREA

We assessed winter nutritional restriction of moose within a 6,068-km² study area located between 47°06'N and 47°58'N latitude and 90°04'W and 92°17'W longitude in northeastern Minnesota (Figure 1). Including bogs, swamps, lakes, and streams; lowland stands of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*); and upland balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), white pine (*P. strobus*), and red pine (*P. resinosa*), this region has been classified as Northern Superior Upland (Minnesota Department of Natural Resources [MNDNR] 2015). Trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and conifers are frequently intermixed.

Wolves (*Canis lupus*) and American black bears (*Ursus americanus*) are predators of moose (Fritts and Mech 1981, Severud et al. 2015) with recent densities estimated at 3.4 wolves and 23 bears/100 km² (Erb and Sampson 2013, Garshelis and Noyce 2015). White-tailed deer (*Odocoileus virginianus*) are managed at pre-fawning densities of <4 deer/km², and are the primary prey of wolves in most of northern Minnesota (Nelson and Mech 1986, DelGiudice et al. 2002). The MNDNR assesses winter severity (1 Nov–31 May) by a winter severity index (WSI), calculated by accumulating 1 point for each day with a temperature $\leq 0^{\circ}\text{F}$ (-17.8°C , temperature-day) and 1 point for each day with snow depth ≥ 15 inches (38.1 cm, snow-day), for a potential total of 2 points per day. Maximum WSI values varied markedly across moose range, 35–160, 184–245, 54–152, 31–142, and 50–159 for winters 2012–13 to 2016–17, respectively (Minnesota State Climatology Office 2017). Mean daily minimum and maximum temperatures varied markedly during November–April from 2012–13 to 2016–17 at Ely, Minnesota (Midwestern Regional Climate Center 2017; Figure 2). The heat stress index (HSI_{Min} and HSI_{Max}) for moose during January and the “cold season” (Nov–Mar) was calculated by daily accumulation of degrees Celsius $> -5^{\circ}\text{C}$ for the maximum and minimum ambient temperatures, respectively (Renecker and Hudson 1986).

METHODS

We collected fresh snow-urine specimens of moose during 6 January–28 March 2013–2017. We conducted snow-urine sampling according to a random design. Our field team drove (by truck or snowmobile) a route of approximately 201 km (125 miles) to distribute the sampling throughout

the study area (Figure 1). Field technicians were not restricted to this route, rather they could deviate, particularly on foot, as dictated by the presence of fresh moose sign (e.g., tracks, urine specimens, pellets). Each field team used handheld GPS units loaded with several land coverages (R. G. Wright, Minnesota Information Technology @ Minnesota Department of Natural Resources, Section of Wildlife) and a Superior National Forest map (U. S. Forest Service) to navigate in the field.

Generally, sampling was conducted within 7 days of a fresh snowfall, most often within 2–4 days, so that we could associate urine chemistry data and nutritional assessments with specific temporal intervals. Upon observing fresh moose sign, technicians tracked the individual(s) on foot as necessary until they found a fresh snow-urine specimen. The objective for the collections was to sample primarily adult (>1 year old) moose (indicated by track and bed size). This was not particularly challenging, because by this time of year calves comprised only 13–17% of the population (DelGiudice 2017). We focused primarily on the adult age class to facilitate optimum comparability of data.

Specimens were collected and handled as described by DelGiudice et al. (1991a, 1997). A GPS waypoint was recorded for each snow-urine specimen collected. Date of the most recent snowfall and comments describing the presence of moose or other sign in the area also were recorded.

Snow-urine specimens were analyzed for UN and C (mg/dL for both) by a Roche Cobas Mira auto-analyzer (Roche Diagnostics Systems, Inc., Montclair, NJ) in the Forest Wildlife Populations and Research Group's laboratory. We used 0.1 and 3.0 mg/dL as reliable thresholds for accurate measuring of C and UN, respectively, for our auto-analyzer; samples with values below these thresholds were excluded (C. Humpal, MNDNR, personal communication). Data were compared as UN:C ratios to correct for differences in hydration, body size, and dilution by snow (DelGiudice 1995, DelGiudice et al. 1988).

Winter (Jan–Mar) was divided into 6, approximately 2-week sampling intervals (1–15 Jan, 16–31 Jan, 1–15 Feb, 16–28 Feb, 1–15 Mar, and 16–31 Mar). Sample sizes for the snow-urine collections varied by interval due to variability of weather (i.e., snow conditions), equipment availability, logistical challenges, and ease of finding samples. Most of the UN:C data are reported by the entire winter or by sampling interval as means (\pm standard error). Additionally, based on past work, urinary UN:C values were assigned to 1 of 3 levels of nutritional restriction: moderate or “normal,” <3.0 mg:mg; moderately severe, 3.0–3.4 mg:mg; and severe, \geq 3.5 mg:mg (DelGiudice et al. 1997, 2001, 2010). We report the percentage of samples with UN:C values falling within each of these categories. We examined relationships between proportions of snow-urine specimens with UN:C values indicative of severe nutritional restriction (\geq 3.5 mg:mg) and population estimates, seasonal survival, and HSI by simple linear regression analyses in Excel (Version 14.0.7153.5000, Microsoft Corporation 2010).

RESULTS AND DISCUSSION

During January–March 2013–2017, a total of 944 urine specimens from moose were collected to assess nutritional status at the population level. Specifically, annual totals of 123, 307, 165, 189, and 160 sufficiently concentrated moose snow-urine samples, respectively, were collected during 5–6, 2-week sampling intervals using our designated routes. The greater number of samples collected during 2014 was largely due to the early and prolonged deep snow cover.

Overall, mean UN:C ratios were 3.7, 2.9, 2.9, 3.5, and 3.7 mg:mg for winters 2013 to 2017, respectively (Figure 3). The mean population UN:C ratio for entire winters 2013, 2016, and 2017 were above the threshold indicative of severe nutritional restriction (i.e., a starvation diet) and

accelerated body protein catabolism. The elevated mean UN:C of 2016 and 2017 were influenced largely by several collected samples that exhibited very high UN:C ratios indicative of a moribund condition (≥ 22.0 mg:mg), given that the proportion of samples in the lowest UN:C category was greatest that year (Figure 4). During 2014 and 2015 the population means were just below the defined moderately severe interval. Additionally, indicative of the unique severity of nutritional restriction in 2013, nearly one-third of all samples collected yielded UN:C ratios ≥ 3.5 mg:mg (Figure 4). The corresponding percentages of winters 2014 to 2017 were notably less than in 2013.

Mean urinary UN:C ratios by 2-week interval of winter 2013 indicated that nutritional restriction was normal or moderate during late-January, but became severe throughout February and early-March, and was still assessed as moderately severe in late-March (Figure 5). As severe nutritional restriction of moose progresses with winter, those animals may be under-sampled as some eventually die, and those still alive urinate less, which is a physiological mechanism to conserve water and electrolytes. Percentage of samples with urinary UN:C ratios indicative of severe nutritional restriction peaked (73.3%) in early-February and remained relatively high through late-March (36%) during 2013 (Figure 6). Such elevated values have been associated with long-term fasting in controlled nutrition studies of captive white-tailed deer and starvation of free-ranging elk (*Cervus elaphus*), bison (*Bison bison*), and moose (DelGiudice et al. 1991a, 1994, 1997, 2001). The percentage of snow-urine specimens in 2013 with UN:C ratios indicative of moderately severe to severe nutritional restriction throughout the winter was 45.5% (Figure 4).

During 2014 mean urinary UN:C ratios in all 2-week intervals, except early February, remained just below the moderately severe category (Figure 5), and the percentage of samples with ratios indicative of severe nutritional restriction gradually decreased as this winter progressed (Figure 6), either due to an easing of conditions restricting access to forage or because severely stressed individuals were being under-sampled, which may be most plausible as previously explained. Adverse effects of the late, but prolonged conditions of winter 2013, including warm temperatures, may have contributed to the high spring-summer calf loss and absence of the need for dams to lactate (Severud et al. 2015). This also may have allowed the surviving animals to rebound nutritionally more quickly and to fare better during winter 2014. This would not be unlike the documented effects on the nutritional status and survival of northern Minnesota deer during the consecutive severe winters of 1996 and 1997 (DelGiudice et al. 2006; G. D. DelGiudice, unpublished data). Overall in winter 2014, UN:C values of 64% of the collected snow-urine samples classified nutritional restriction as moderate (normal), whereas 36% reflected moderately severe to severe restriction, which was less than in 2013 (Figure 4). Similar to winter 2014, severe nutritional restriction of moose was not as prevalent in 2015 as in 2013, but it was up slightly compared to 2014 (Figure 4). However, a higher percentage of moose appeared to be experiencing moderate or normal restriction and a smaller percentage moderately severe than in 2013 and 2014 (Figure 4). Rapidly diminishing snow cover prevented collection of snow-urine samples or assessments during the last 2 weeks of March 2015, certainly a positive factor relative to moose nutrition at that time. Unexpectedly, both 2016 and 2017 had the greatest percentage of samples with urinary UN:C ratios indicative of moderate nutritional restriction (70.4% and 70.6%, respectively) and the smallest percentage indicative of severe nutritional restriction (Figure 4), despite having the highest HSI values calculated with daily maximum (958 and 833) or minimum (220 and 194) ambient temperatures.

According to maximum WSI values, winter 2014 was the most severe of the 5 in northeastern Minnesota moose range, followed by 2013, 2017, 2015, and 2016. Although the WSI numbers have value for annual comparisons of winter conditions, this WSI formula has far greater relevance to the size and energetics of white-tailed deer than for the much larger moose,

which are not hindered as much by deep snow (DelGiudice et al. 2002, 2006; Schwartz and Renecker 2007). Furthermore, while the accumulation of snow-days and temperature-days has proven significant relative to the survival of white-tailed deer (DelGiudice et al. 2002), actual snow depth, its temporal occurrence, and duration may be of equal or greater importance for moose and deer (Telfer and Kelsall 1984, DelGiudice 1998, DelGiudice et al. 2002, Schwartz and Renecker 2007). During 2013, conditions became severe during mid- to late-winter; consequently, a high number of snow-days did not accumulate, but the season was prolonged. The severe nutritional restriction of moose in 2013 was most similar to that which occurred in moose during several winters (1988–1990) on Isle Royale associated with severe winter tick infestations and steep population decline (DelGiudice et al. 1997). Abundant evidence from the field in the MNDNR's ongoing studies similarly indicated that the winter tick infestation of moose in northeastern Minnesota was notably more severe during winter 2013 than in any of those that followed through 2017 (Carstensen et al. 2014; M. Carstensen, MNDNR, personal communication).

Perhaps the ultimate value to management of assessments of nutritional status of free-ranging animals comes when the findings can be related to the performance and dynamics of the population and other ecological factors challenging that performance (DelGiudice et al. 1997, Cook et al. 2004). Our population-level nutritional assessments continue to closely track ($r^2 = 0.75$) population estimates of moose from the annual aerial survey (Figure 7). What is most clear is that although restriction varies among the 5 winters, elevated UN:C values suggest a level of nutritional deprivation not supportive of positive population performance or growth. During 2013 to 2015, warming winter temperatures appeared to be having the most pronounced influence on the nutritional status of moose. As the January and winter HSI_{Max} values increased, the incidence of severe nutritional restriction of moose increased ($r^2 \geq 0.93$, DelGiudice and Severud 2017), which we believed may have led to many of these animals becoming more vulnerable to various health-related causes of mortality and predation (Carstensen et al. 2015). Similar relationships were noted between winter nutritional restriction, winter tick epizootics, and decreasing moose numbers on Isle Royale (DelGiudice et al. 1997). But, something unexpected occurred when data from winters 2016 and 2017 (the warmest winters since 2013 in northeastern Minnesota) were incorporated into the analyses. The strong relationships between HSI_{Max} of January and winters 2013–2015 and severe nutritional restriction collapsed; the incidence of severe nutritional restriction of moose was still noteworthy in 2016 and 2017, but was the lowest of the 5 winters. However, the incidence of severe nutritional restriction at the population level remained inversely related to variation of *natural* winter ($r = -0.86$) and winter-summer ($r = -0.88$) survival rates of GPS-collared adult moose (Figure 8). Importantly, because these latter relationships are consistent with our association of severe nutritional restriction with the population estimates, it suggests that the current study cohort of GPS-collared moose is indeed representative of the free-ranging population in northeastern Minnesota. While these aforementioned relationships do not substantiate cause-and-effect, a preponderance of the empirical evidence is suggesting that winter nutritional restriction is a critical factor influencing the performance and dynamics of the northeastern moose population. Clearly, there is still much to understand about these relationships. New to this understanding are the effects of variation in severe nutritional restriction and the loss of breeding females on annual calf production (Figure 9).

In addition to the multi-year occurrence of severe nutritional restriction of moose, preliminary analyses reveal a vast spatial distribution throughout moose range of collected snow-urine samples with UN:C ratios indicative of severe nutritional deprivation (Figure 10). The wide temporal and spatial distributions of severe nutritional restriction suggest that habitat deficiencies at the landscape scale may constitute a primary contributing factor. We continue to apply significant efforts into investigating the habitat-nutrition relationships, but habitat

deficiencies related to forage availability and quality, vegetative species composition, or less-than-optimum arrangements of forage openings and forest stands affording seasonal thermal cover remain unclear. Data from future winter nutritional assessments are required to provide additional support for our conclusions or to refute them. But the current data set, in combination with data from other ongoing habitat and nutritional studies, should provide a basis for formulating management recommendations that may be implemented and evaluated in the near future.

ACKNOWLEDGMENTS

We thank B. Smith for his monitoring of weather and HSI data, B. Matykiewicz, J. Ostroski, L. Kruse, M. Bowman, D. Dewey, R. Willaert, B. Smith, R. Ryan, R. Peterson, C. Olson, and K. Foshay for their dedication and strong efforts necessary to sampling these free-ranging moose, and R. Wright for contributing his GIS skills. We also are grateful to T. Rusch, D. Plattner, M. Meskill, L. Cassioppi, M. Magnuson, and N. Thom for their assistance and cooperation in setting up office space and securing key equipment. We appreciate and acknowledge the laboratory support and skills of C. Humpal. This study was supported largely by the Minnesota Environmental and Natural Resources Trust Fund (ENRTF), the Wildlife Restoration (Pittman-Robertson) Program, and the Minnesota Department of Natural Resources Section of Wildlife, with supplemental funding from the Minnesota Deer Hunters Association.

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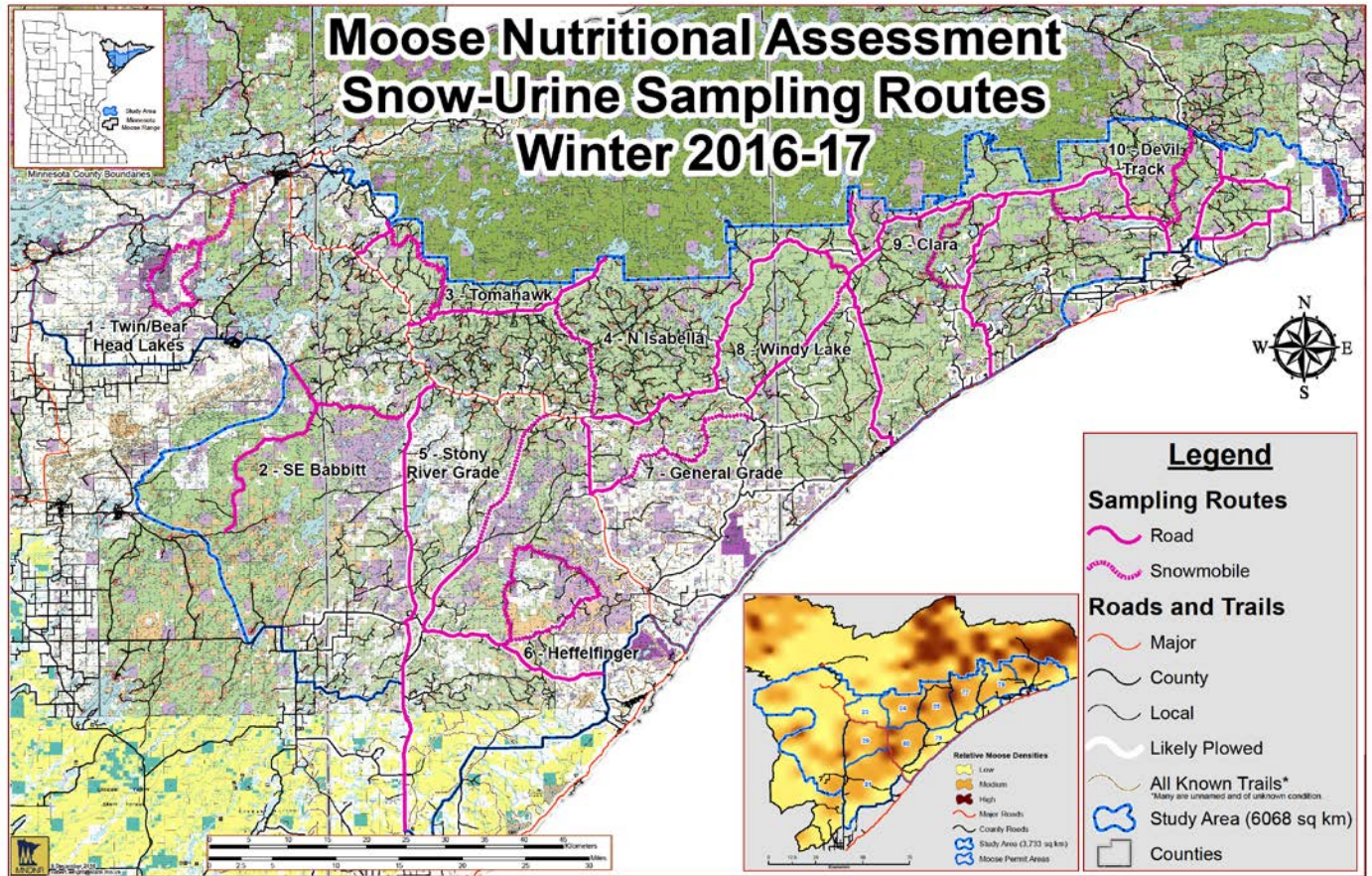


Figure 1. Map depicting the moose study area in northeastern Minnesota and the routes (i.e., roads and snowmobile trails in purple) used to distribute the sampling of fresh moose urine in snow (snow-urine) for nutritional assessments throughout the area, January–March 2013–2017.

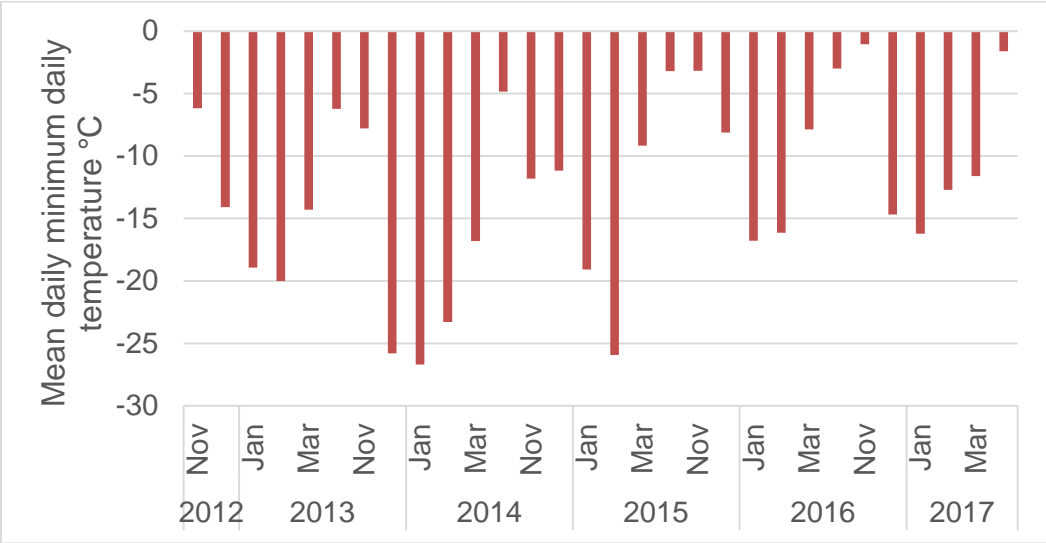
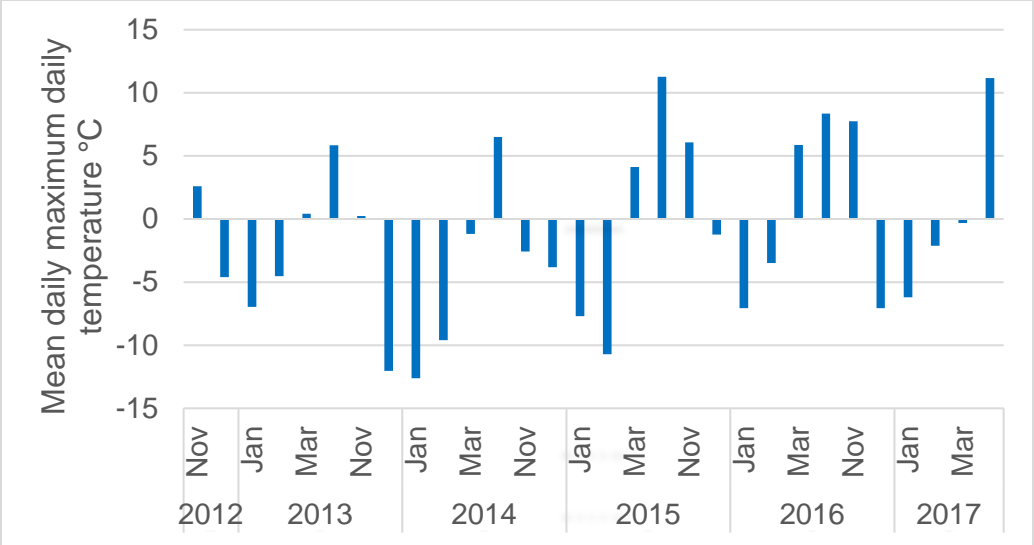


Figure 2. Mean daily maximum (top) and minimum (bottom) ambient temperatures, Ely, Minnesota, November–April 2012–2017 (Midwestern Regional Climate Center 2017).

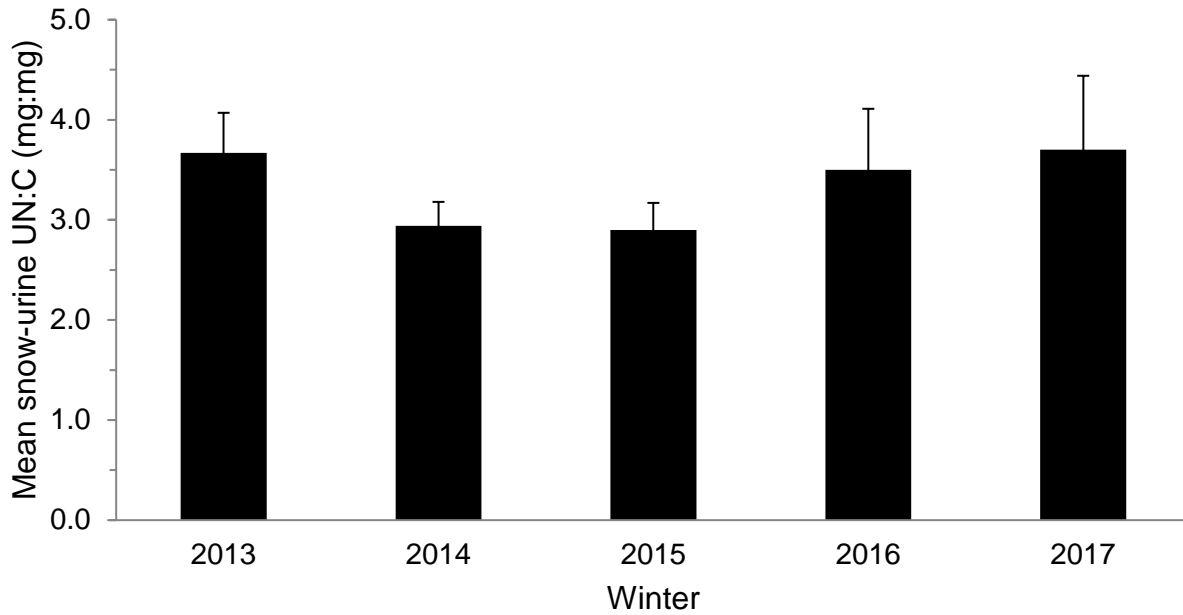


Figure 3. Overall mean (+ SE) urea nitrogen:creatinine (UN:C) ratios of samples of fresh urine voided in snow (snow-urine) by moose and serially collected for assessments of nutritional restriction throughout northeastern Minnesota, January–March 2013–2017.

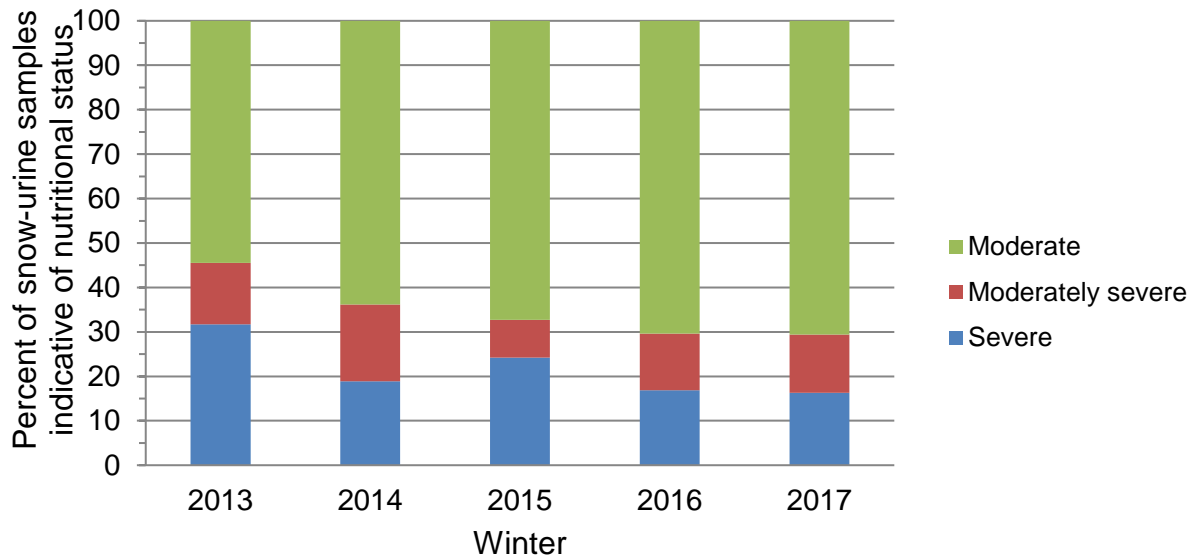


Figure 4. Overall percent of serially collected moose urine samples voided in snow (snow-urine) with urea nitrogen:creatinine (UN:C) ratios indicative of moderate/normal (UN:C <3.0 mg:mg), moderately severe (UN:C = 3.0–3.4 mg:mg), and severe nutritional restriction (UN:C ≥3.5 mg:mg) throughout northeastern Minnesota, January–March 2013–2017.

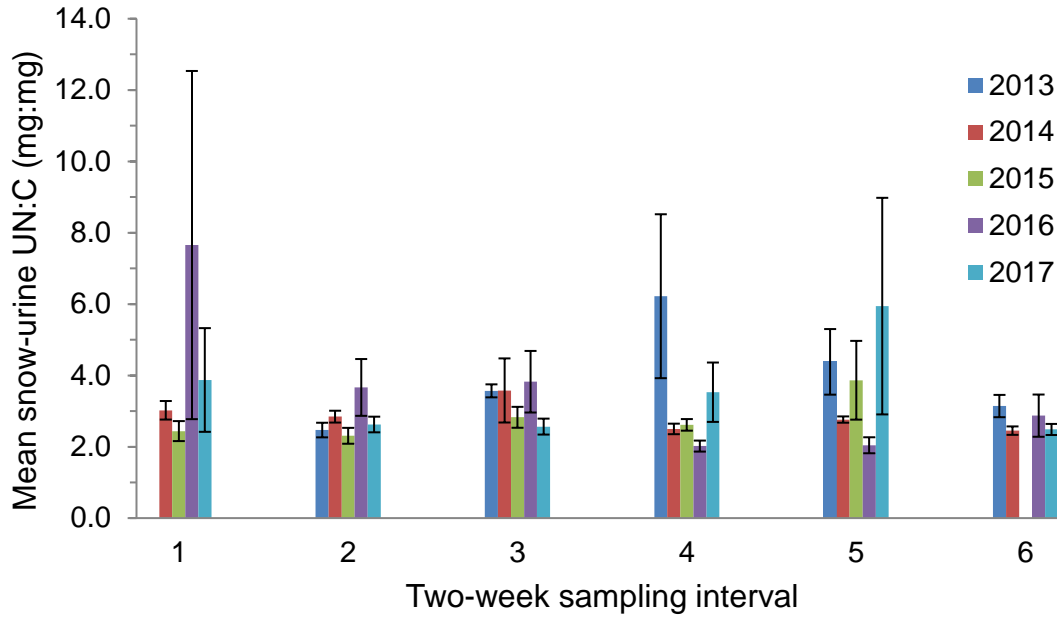


Figure 5. Mean (\pm SE) urea nitrogen:creatinine (UN:C) ratios of samples of fresh urine voided in snow (snow-urine) by moose and collected during 2-week sampling intervals for assessments of nutritional restriction throughout northeastern Minnesota, January–March 2013–2017.

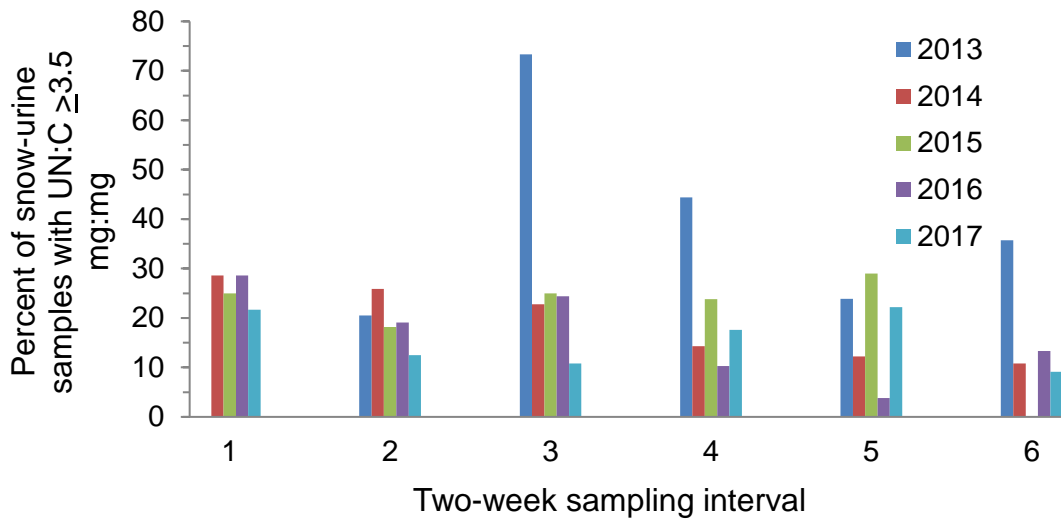


Figure 6. Percent of fresh urine samples voided in snow (snow-urine) by moose and collected during 2-week intervals with urea nitrogen:creatinine (UN:C) ratios indicative of severe nutritional restriction (UN:C \geq 3.5 mg:mg) throughout northeastern Minnesota, January–March 2013–2017.

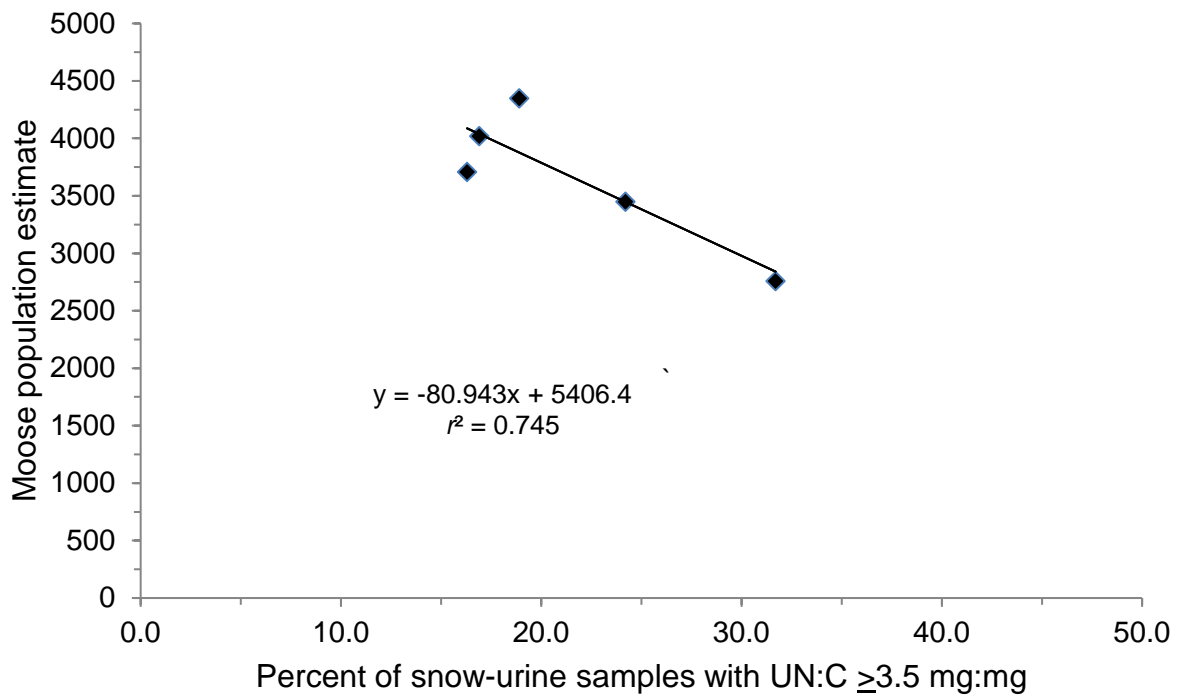


Figure 7. Relationship of the incidence of severe winter nutritional restriction of moose, indicated by the percentage of collected samples of urine in snow (snow-urine) with urea nitrogen:creatinine (UN:C) ratios ≥ 3.5 mg:mg, to annual population estimates of moose in northeastern Minnesota (estimates from DelGiudice 2017), January–March 2013–2017.

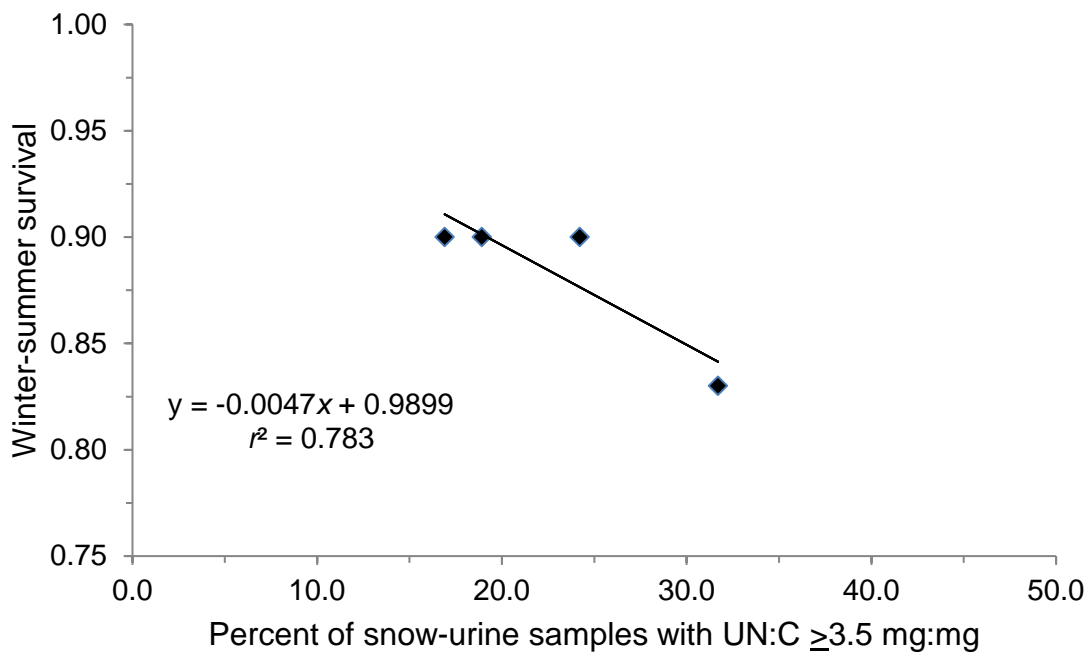
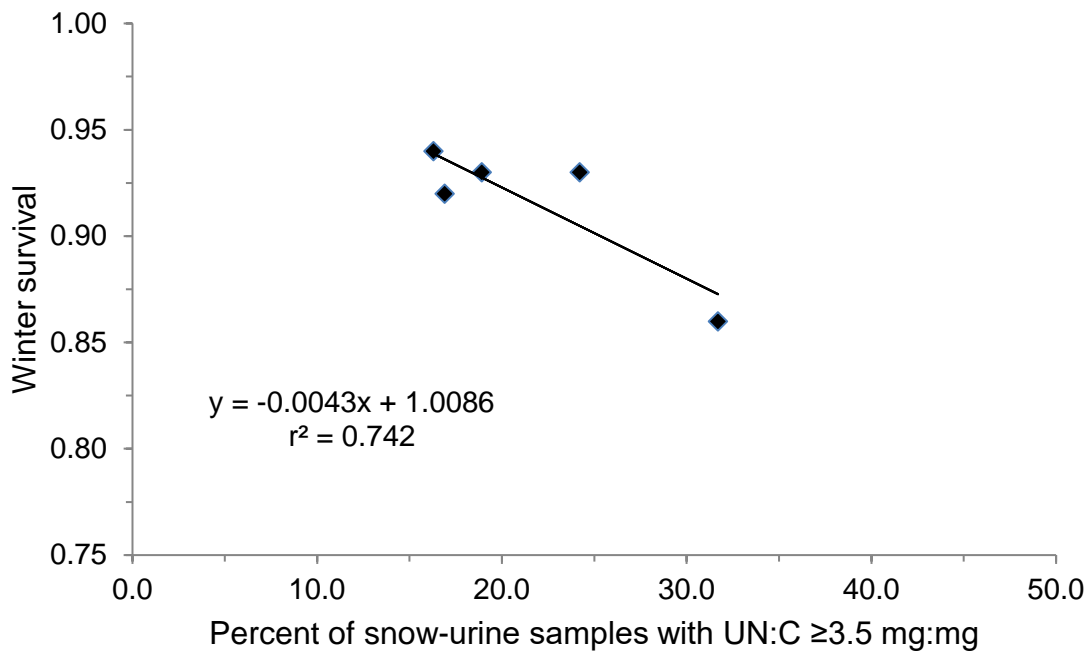


Figure 8. Relationships of the incidence of severe winter nutritional restriction of moose at the population level, indicated by the percentage of collected samples of urine in snow (snow-urine) with urea nitrogen:creatinine (UN:C) ratios \geq 3.5 mg:mg, to winter (top, 1 Nov–31 May 2013–2017) and winter-to-summer (bottom, 1 Nov–31 Aug 2013–2016) survival of GPS-collared adult moose in northeastern Minnesota.

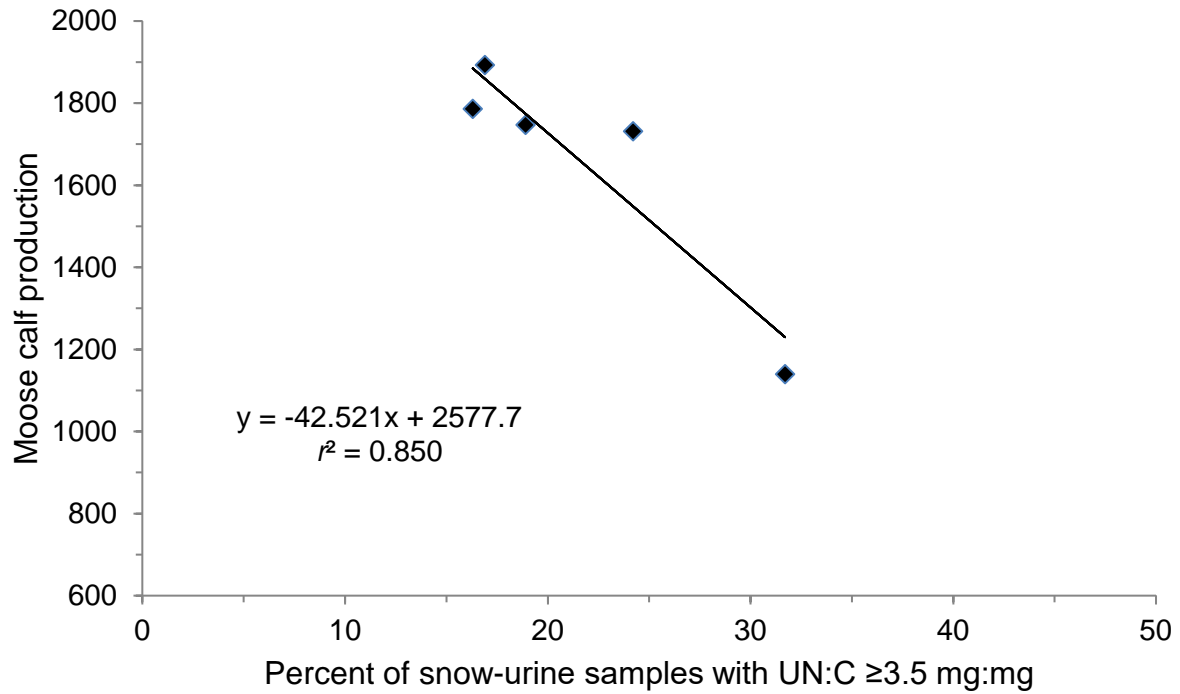


Figure 9. Relationships of the incidence of severe winter nutritional restriction of moose, indicated by the percentage of collected samples of urine in snow (snow-urine) with urea nitrogen:creatinine (UN:C) ratios ≥ 3.5 mg:mg, to annual calf production, northeastern Minnesota, 2013–2017.

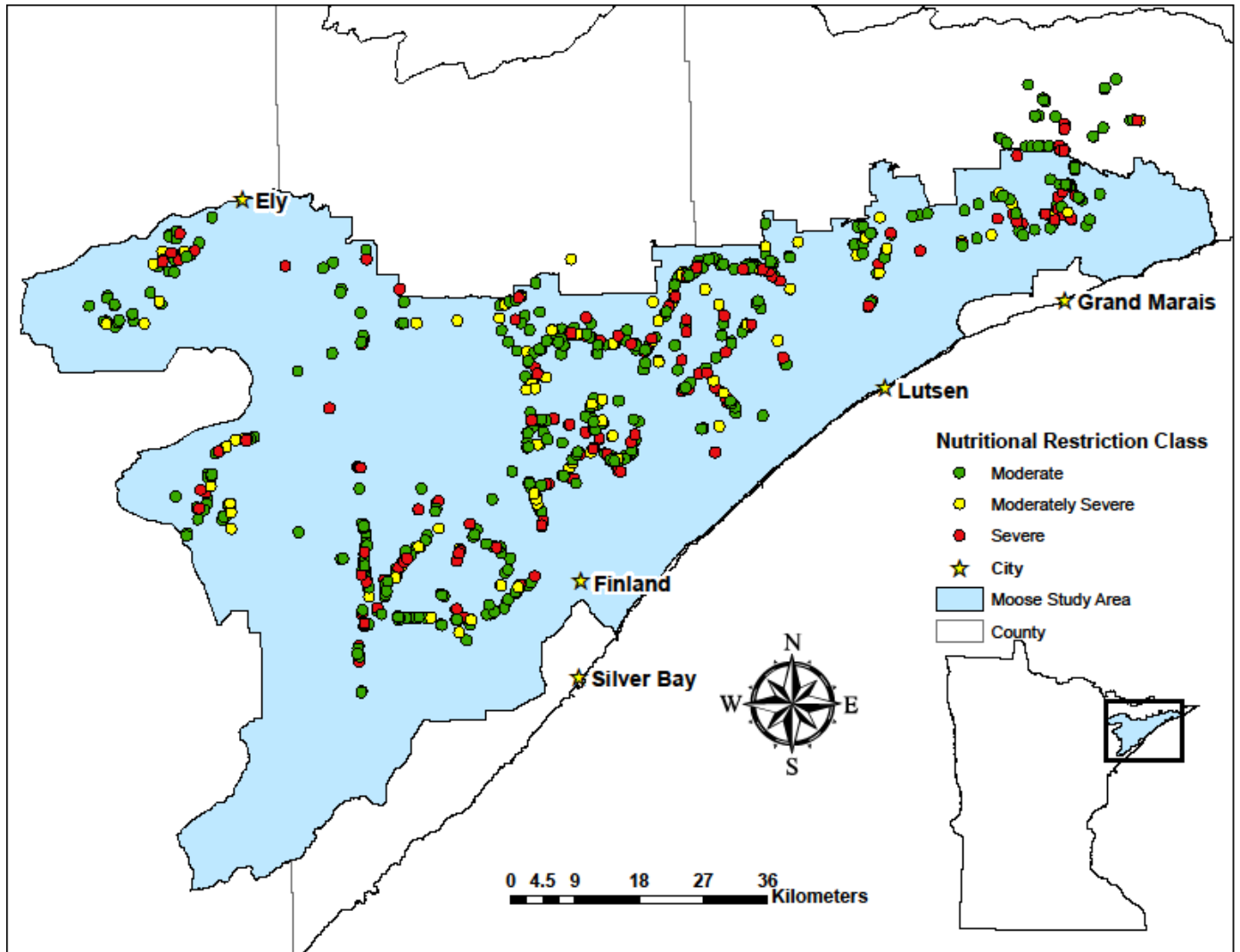


Figure 10. Spatial distribution of fresh urine samples of moose, serially collected for chemical analysis to assess the severity of winter nutritional restriction. Urinary urea nitrogen:creatinine (UN:C) ratios of <3.0 , $3.0\text{--}3.4$, and ≥ 3.5 mg:mg are indicative of moderate/normal (green), moderately severe (yellow), and severe (red) nutritional restriction, northeastern Minnesota, 6 January–28 March 2013–2017.