WINTER NUTRITIONAL RESTRICTION AND DECLINE OF MOOSE IN NORTHEASTERN MINNESOTA, WINTERS 2013–2019

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SUMMARY OF FINDINGS

The moose (*Alces alces*) population in northeastern Minnesota has declined an estimated 53% from 2006 to 2019. As was the case in northwestern Minnesota's moose decline during mid-1980−2007, 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 4 January–22 March 2013–2019, we collected annual totals of 123, 307, 165, 189, 160, 332, and 190 moose snow-urine samples, respectively, and mean seasonal UN:C ratios were 3.7, 2.9, 2.9, 3.5, 3.7, 2.6, and 2.3 mg:mg for the 7 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, 2015, 2018, and 2019 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 is realized when the findings can be related to the performance and dynamics of the population and other ecological factors challenging that performance. Through 2017, our population-level nutritional assessments were closely tracking separate population estimates ($r^2 = 0.75$) of moose in northeastern Minnesota. However, this relationship weakened with the inclusion of the 2018 and 2019 population estimates and snow-urine data. This likely was attributable in part to the notable uncertainty associated with the annual population estimates and its continued statistical stability, but apparent decline. Biologically, the mean population-level UN:C ratio (2.6 and 2.3) and relatively low incidence of snow-urine samples with UN:C ratios indicative of severe nutritional restriction (14.8% and 6.8%) were consistent with the population's continued stability. Although nutritional restriction varied among the 7 winters, data suggested a level of deprivation not supportive of population 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 first 5 winters (the only years for which survival estimates are available), we documented that the level of severe nutritional restriction was inversely related ($r = -0.86$) to variation of *natural* winter survival of global positioning system (GPS)-collared adult moose. While these relationships do

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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.

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 2019 population (4,180 moose) is 53% less than in 2006 (8,840 moose, DelGiudice 2019), exhibiting a trajectory similar to that documented previously for moose in northwestern Minnesota, where the population decreased from about 4,000 in the mid-1980s to <100 moose by 2007 (Murray et al. 2006). Furthermore, mean annual mortality rates of collared adult moose associated with the declines were similarly high (21%) in the northwest and northeast (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 (2013–2017) aggressive study of global positioning system (GPS)-collared adult moose reported a mean annual mortality rate of 14.7%, 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 being well-documented (Carstensen et al. 2018). 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).

Temperature-survival relationships are complex, and indicate that climate change can directly and indirectly impact ungulate populations (Bastille-Rousseau et al. 2016, 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^o to 24^o C during summer and $–5^o$ 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, McCann et al. 2016, 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 relative to adult and juvenile survival, subsequent reproductive success, and population dynamics (Robbins 1993; DelGiudice 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. 1991*a*,*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 (body) 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, Michigan, 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 winter progresses; and

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.

We hypothesized that increasing winter ambient temperatures, exceeding the HSI threshold, are contributing to the severity of nutritional restriction and energy deficit of moose. We also predicted that the severity of nutritional restriction would be inversely related to the performance of the population in northeastern Minnesota, primarily through its effect on adult survival and possibly calf production. 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-km^2 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 4.0 wolves and 23 bears/100 km^2 (Garshelis and Noyce 2015, Erb et al. 2017). White-tailed deer (*Odocoileus virginianus*) are managed at pre-fawning densities of <4 deer/km^2, 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 November–31 May) by a Winter Severity Index (WSI), calculated by accumulating 1 point for each day with a temperature ≤−17.7^{o} C (0^{o} F, temperature-day) and 1 point for each day with snow depth ≥38 cm (15 inches, snow-day), for a potential total of 2 points per day. Maximum WSI values varied markedly across moose range, with values of 35–160, 184–245, 54–152, 31–142, 50−159, 50−179, and 100−159 for winters

2012–2013 to 2018–2019, respectively (Minnesota State Climatology Office 2018). Mean daily minimum and maximum temperatures varied markedly during November–April from 2012–2013 to 2018–2019 at Ely, Minnesota (Midwestern Regional Climate Center 2019; Figure 2). The heat stress index (HSI_{Min} and HSI_{Max}, see Figure 3) for moose during the "cold season" (November–March) was calculated by daily accumulation of degrees Celsius exceeding -5^{o} C for the maximum and minimum ambient temperatures, respectively (Renecker and Hudson 1986).

METHODS

We collected fresh snow-urine specimens of moose during 3 January−22 March 2013− 2019. Our field team drove (by truck or snowmobile) a route of approximately 201 km 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 @ MNDNR, Section of Wildlife) and a Superior National Forest map (US 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 narrow 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 (≥1.5 yr) 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 2019). We focused primarily on the adult age class to facilitate optimum comparability of physiological assessment data.

Specimens were collected and handled as described by DelGiudice et al. (1991*a*, 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, New Jersey) in the Forest Wildlife Populations and Research Group's laboratory. We used 0.1 and 3.0 mg/dL as reliable threshold concentrations for accurately measuring C and UN, respectively, with our auto-analyzer; samples with values below these thresholds were excluded (C. A. Humpal, MNDNR, personal communication). Data were compared as UN:C ratios to correct for differences in hydration, body size, and dilution by snow (DelGiudice et al. 1988, DelGiudice 1995).

Winter (January–March) was divided into 6, 2-week sampling intervals (~1–15 January, 16–31 January, 1–14 February, 15–28 February, 1–15 March, and 16–31 March). 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 (± 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, ≥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 (≥3.5 mg:mg) and populations 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 2013–2019, 1,479 urine specimens from moose were collected and analyzed to assess nutritional status at the population level. Specifically, annual totals of 123, 307, 165, 189, 160, 332, and 190 moose snow-urine samples, respectively, were collected during 5–6, 2-week sampling intervals using our designated routes and were adequately concentrated for chemical analysis. The greater number of samples collected during 2014 was largely due to the early and prolonged deep snow cover, whereas during 2018, the greatest number of samples was attributable to more intense sampling during the middle of the winter sampling period.

Overall, mean UN:C ratios were 3.7, 2.9, 2.9, 3.5, 3.7, 2.6, and 2.3 mg:mg for winters 2013 to 2019, respectively (Figure 4). The mean population UN:C ratio for entire winters 2013, 2016, and 2017 were above the threshold indicative of severe nutritional restriction or a starvation diet (≥3,5 mg:mg) and accelerated body protein catabolism. But the elevated mean UN:C of 2016 and 2017 were influenced largely by a small number of collected samples that exhibited very high UN:C ratios indicative of a moribund condition (≥22.0 mg:mg), whereas during 2013, nearly one-third of all samples collected yielded UN:C ratios indicative of severe nutritional restriction (≥3.5 mg:mg, Figure 5). According to Figure 5 and the summed proportions of samples with UN:C ratios indicative of moderately severe and severe restriction, it appears that winters 2013 to 2015 were the most nutritionally challenging to moose, whereas during winters 2016 to 2019, UN:C ratios more consistently indicated moderate restriction to be most common.

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 6). As severe nutritional restriction of moose progresses with winter, those animals may be under-sampled as some eventually die directly from undernutrition or because they have become predisposed to another proximate cause of mortality (e.g., wolf predation, Carstensen et al. 2018), and those still alive urinate less, which is a physiological mechanism to conserve water and electrolytes. However, the 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 7). 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. 1991*a*, 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 5).

During 2014, mean urinary UN:C ratios in all 2-week intervals, except early February, remained just below the moderately severe category (Figure 6), and the percentage of samples with ratios indicative of severe nutritional restriction gradually decreased as this winter progressed (Figure 7), 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 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 from moose classified nutritional restriction as moderate (normal), whereas 36% reflected moderately severe to severe restriction, which was less than in 2013 (Figure 5). 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 5). However, a higher percentage of moose appeared to be experiencing moderate or normal restriction and a smaller percentage moderately severe restriction than in 2013 and 2014 (Figure 5). 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. Interestingly, the greatest percentage of samples (87%) reflecting moose experiencing moderate nutritional restriction occurred during winter 2018–2019, which corresponded with an apparent but not statistically significant increase (38%) in the estimated moose population. In an attempt to better understand within-winter temporal patterns of nutritional restriction across years, we will be conducting more detailed analyses of UN:C data relative to the temporal and spatial distributions of sampling, progressive winter conditions, and sample size.

According to maximum WSI values, winter 2014 was the most severe of the 7 in northeastern Minnesota's moose range, followed in order of severity by 2018, 2019, 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. Severe nutritional restriction of moose in 2013 was most similar to that which occurred in moose during several winters (1988–1990) on Isle Royale, also associated with severe winter tick infestations and a 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 2019 (Carstensen et al. 2014; M. Carstensen, MNDNR, personal communication).

Perhaps the ultimate value of nutritional assessments of free-ranging animals to management comes when the findings are related to the performance and dynamics of the population and other ecological factors challenging that performance (DelGiudice et al. 1997, Cook et al. 2004). During the first 5 years, our nutritional assessments closely tracked population estimates of moose from the annual aerial survey ($r^2 = 0.75$, DelGiudice et al. 2018). With the addition of the 2018 survey results and nutritional assessment data the relationship weakened markedly ($r^2 = 0.27$), but with inclusion of the 2019 data, that relationship has strengthened somewhat ($r^2 = 0.38$, Figure 8). This is likely due to several factors. First, there is a great deal of uncertainty (wide 90% confidence intervals) associated with the annual estimates of moose numbers (DelGiudice 2019). Second, there are spatial and temporal incongruences between data collection for the population estimates versus for the nutritional assessments. Relatively-speaking, the ~9-day aerial survey provides a population estimate that is a winter "snapshot," whereas sample collections for the nutritional assessments span early to late winter (90 days). Finally, we do not yet understand the timeframe associated with potential biological effects on these moose of variation in nutritional restriction within a season or the specific mechanisms involved. It is noteworthy that our population estimates indicate that moose numbers have been relatively stable since 2012, with the exception of 2013. During this winter the population appeared to decrease abruptly; however, general survey conditions were poor, and we could not quantify their potential influence as an artifact on the point estimate. Of the 7 winters, 2013 was the only one in which a severe winter tick infestation occurred and had uniquely strong nutritional consequences for moose at the population level, reflected by urinary UN:C ratios (Figure 5). As described earlier, this has been similarly documented on Isle Royale (DelGiudice et al. 1997). The incidence of samples with UN:C indicative of moderately severe to severe restriction was greatest during winters 2013−2015, whereas during 2016−2019, nutritional restriction has remained remarkably moderate and stable. Six points is the minimum number required for valid statistical assessments of these relationships (F. Martin, Department of Applied Statistics, University of Minnesota, personal communication). Presently, what appears most clear across years is that elevated UN:C values suggest a level of nutritional deprivation not supportive of positive population performance or growth. That said, the lowest percentage of annual samples indicative of moderately severe and severe nutritional restriction occurred during winter 2018−2019 and were associated with an increase (38%) in the estimated number of moose. Continued monitoring of population performance and dynamics and winter nutritional status, and primary factors influencing them, will increase our sample size and continue to improve our understanding of the mechanisms involved.

During 2013 to 2015, warming winter temperatures were strongly associated with variation in 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). We believe that may have led to many of these animals becoming more vulnerable to predation and various health-related causes of mortality (DelGiudice et al. 1997, Carstensen et al. 2015). However, unexpectedly in 2016 and 2017, the years with the highest winter HSI values calculated with daily maximum (958 and 833) or minimum (220 and 194) ambient temperatures were associated with the smallest percentage of samples with UN:C ratios reflecting severe nutritional restriction and greatest percentage indicative of moderate restriction (Figure 5). Overall, the relationship between winter HSI_{Max} or HSI_{Min} and severe nutritional restriction collapsed. Absence of apparent relationships continued through winter 2019. However, the incidence of severe nutritional restriction at the population level remained inversely related to variation of *natural* winter survival (r = –0.86, P = 0.061) but not significantly related to winter-summer survival (r = −0.65, P = 0.231) of GPS-collared adult moose (Figure 9). Survival data collection was temporally more consistent (than population survey data) with data collection for the nutritional assessments, and both data sets have a high level of certainty. Unfortunately, completion of the 5-year study of adult moose did not permit a winter survival estimate for the sixth year. However, importantly, the 5-year relationship of winter nutritional restriction to winter survival supports a reasonably strong biological explanation of the winter nutritional influence on the population trajectory, and it suggests that the study cohort of GPS-collared moose was indeed representative of the free-ranging population in northeastern Minnesota. Clearly, there is still much to understand about these relationships.

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 specimens 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.

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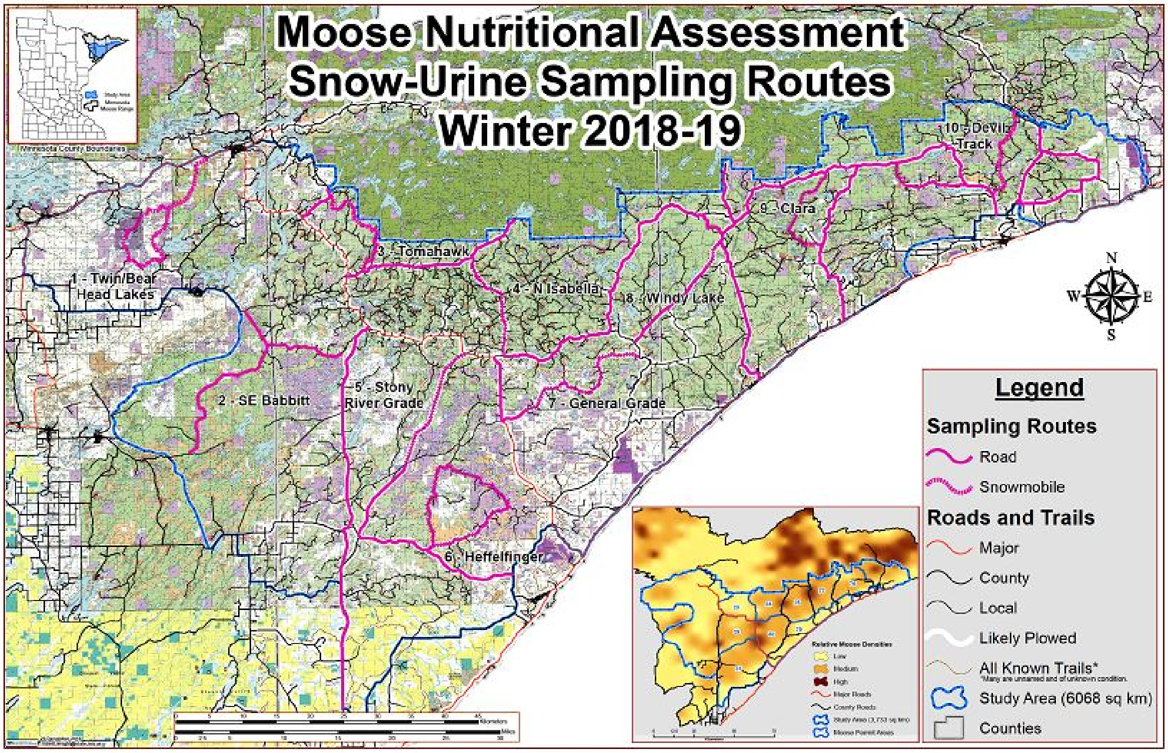
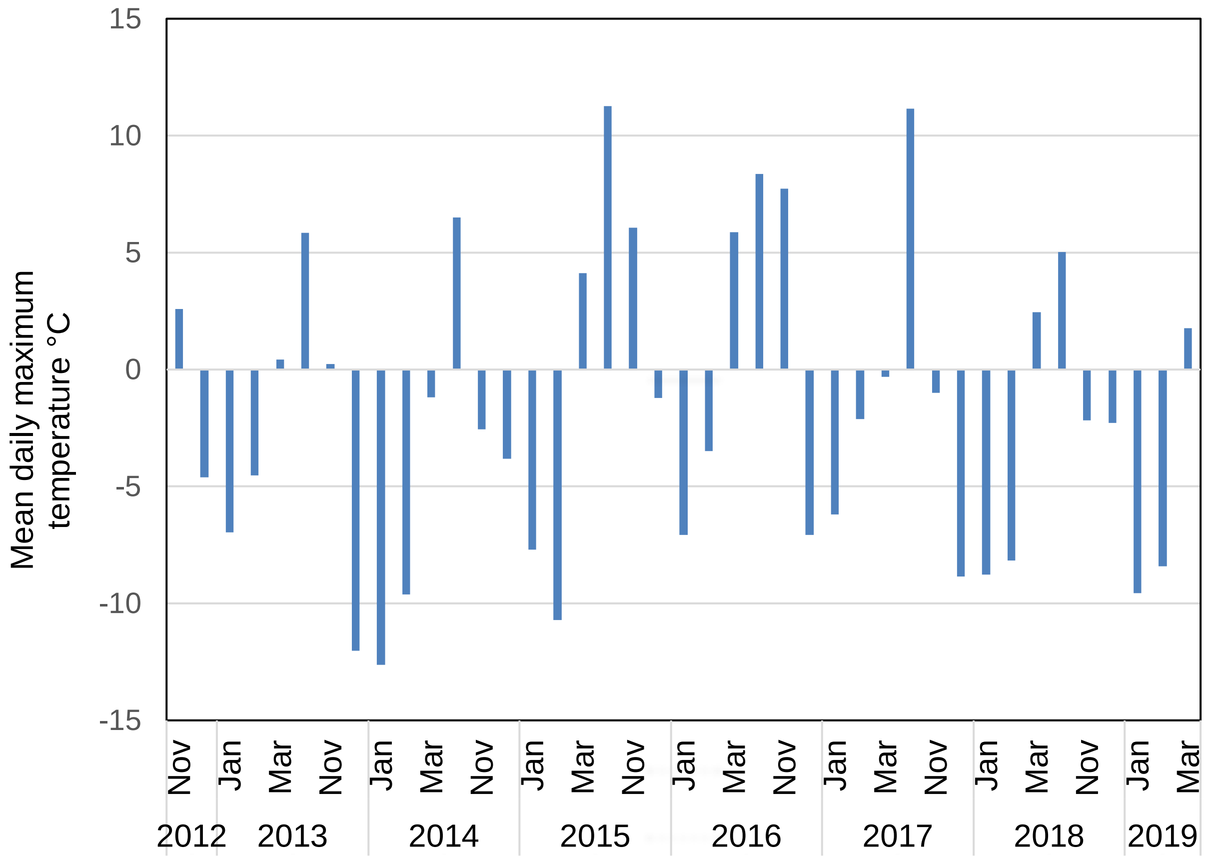


Figure 1. Map depicting the moose study area in northeastern Minnesota and the routes (i.e., roads and snowmobile trails in purple) used to distribute the sampling of fresh moose urine in snow (snow-urine) for nutritional assessments throughout the area, January–March 2013–2019.


Mean daily maximum temperature °C
15
10
5
0
-5
-10
-15
Nov
Jan
Mar
Nov
Jan
Mar
Nov
Jan
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Nov
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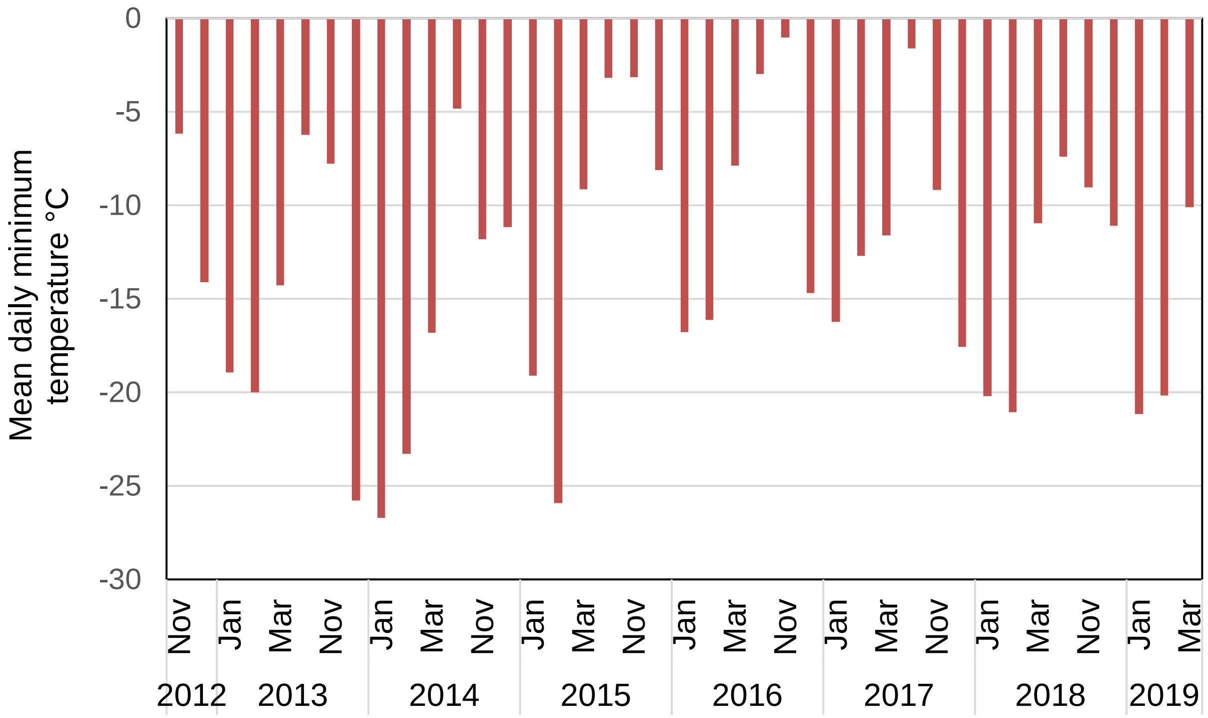
2016
2017
2018
2019


Mean daily minimum temperature °C
0
-5
-10
-15
-20
-25
-30
Nov
Jan
Mar
Nov
Jan
Mar
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Jan
Mar
Nov
Jan
Mar
Nov
Jan
Mar
Nov
Jan
Mar
Nov
Jan
Mar
2012
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Figure 2. Mean daily maximum (top) and minimum (bottom) ambient temperatures, Ely, Minnesota, November–April 2012–2019 (Midwestern Regional Climate Center 2019).

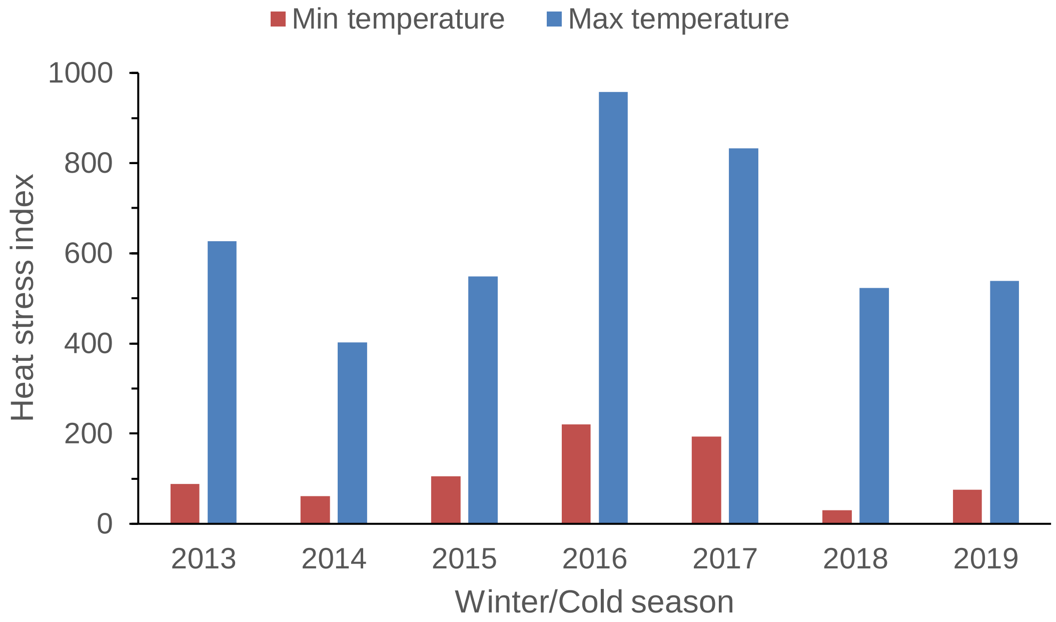

Figure 3. Winter heat stress index (HSI) for moose, calculated by accumulating daily ^{o} C exceeding a −5^{o} C threshold for the minimum and maximum ambient temperatures (1 November−31 March, Renecker and Hudson 1986, 1990) in northeastern Minnesota, 1 November−31 March 2012−2019.

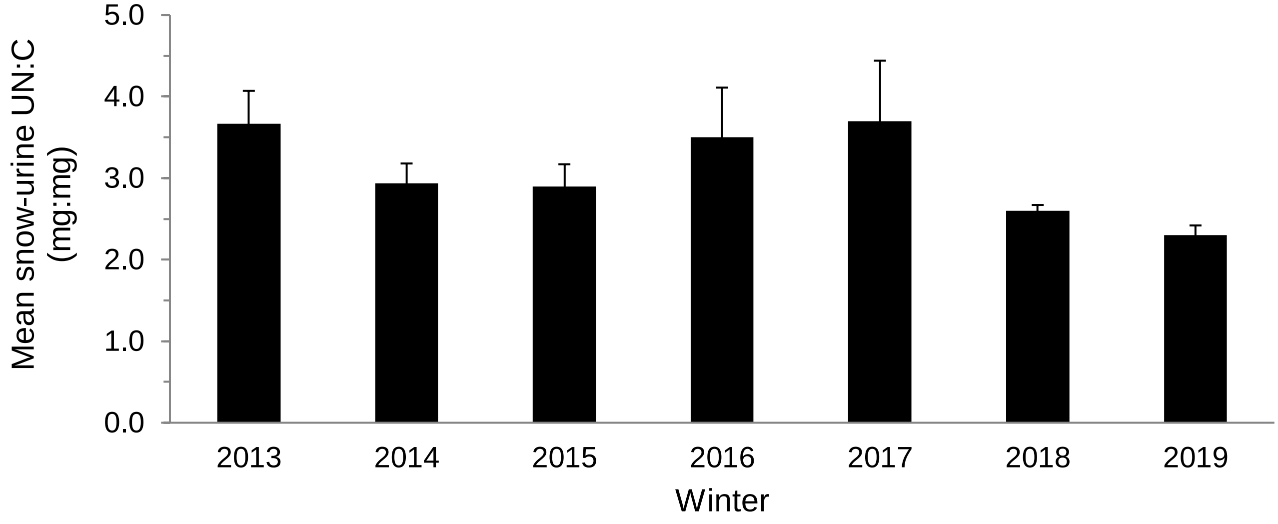

Figure 4. Overall mean (+SE) urea nitrogen:creatinine (UN:C) ratios of samples of fresh urine voided in snow (snow-urine) by moose and serially collected for assessments of nutritional restriction throughout northeastern Minnesota, January–March 2013–2019.

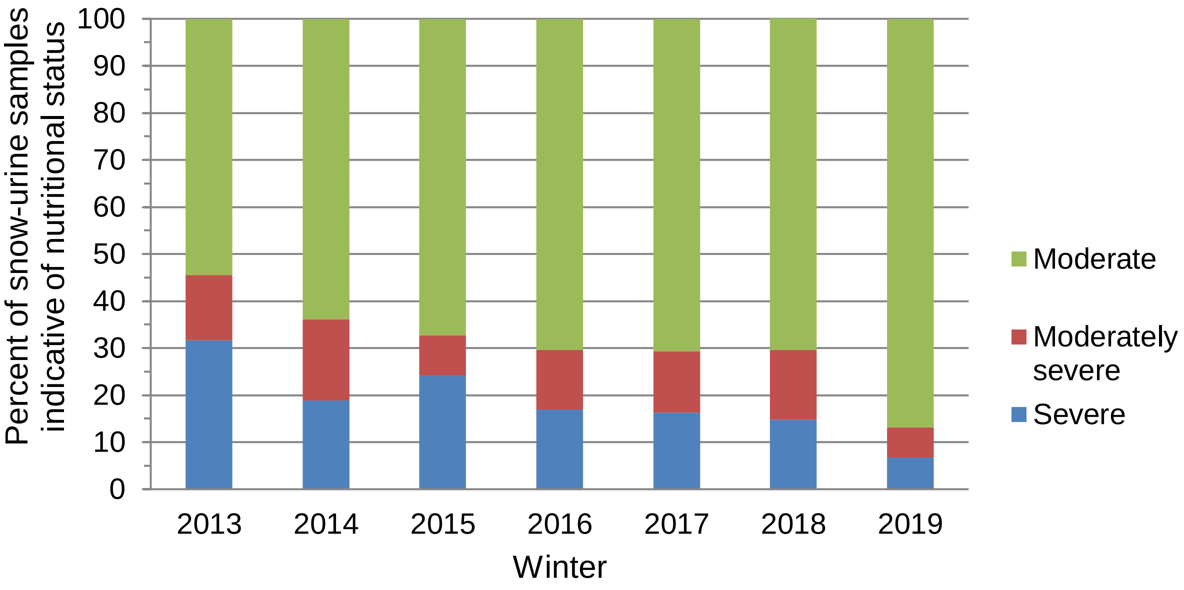

Figure 5. Overall percent of serially collected moose urine samples voided in snow (snow-urine) with urea nitrogen:creatinine (UN:C) ratios indicative of moderate/normal (UN:C <3.0 mg:mg), moderately severe (UN:C = 3.0–3.4 mg:mg), and severe nutritional restriction (UN:C ≥3.5 mg:mg) throughout northeastern Minnesota, January–March 2013–2019.

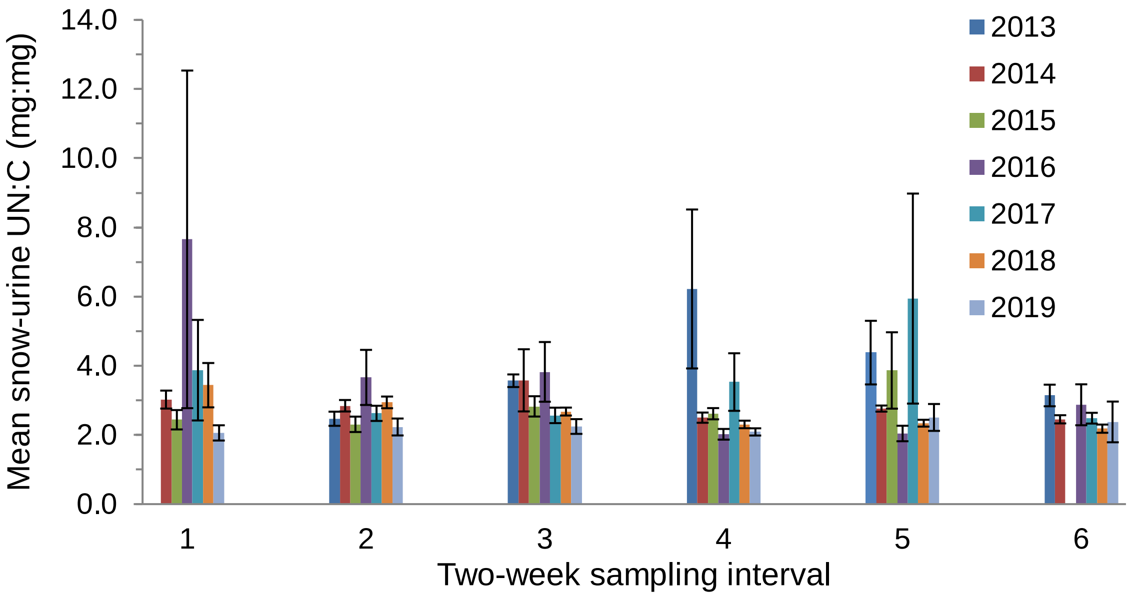

Figure 6. Mean (±SE) urea nitrogen:creatinine (UN:C) ratios of samples of fresh urine voided in snow (snow-urine) by moose and collected during 2-week sampling intervals for assessments of nutritional restriction throughout northeastern Minnesota, January–March 2013–2019.

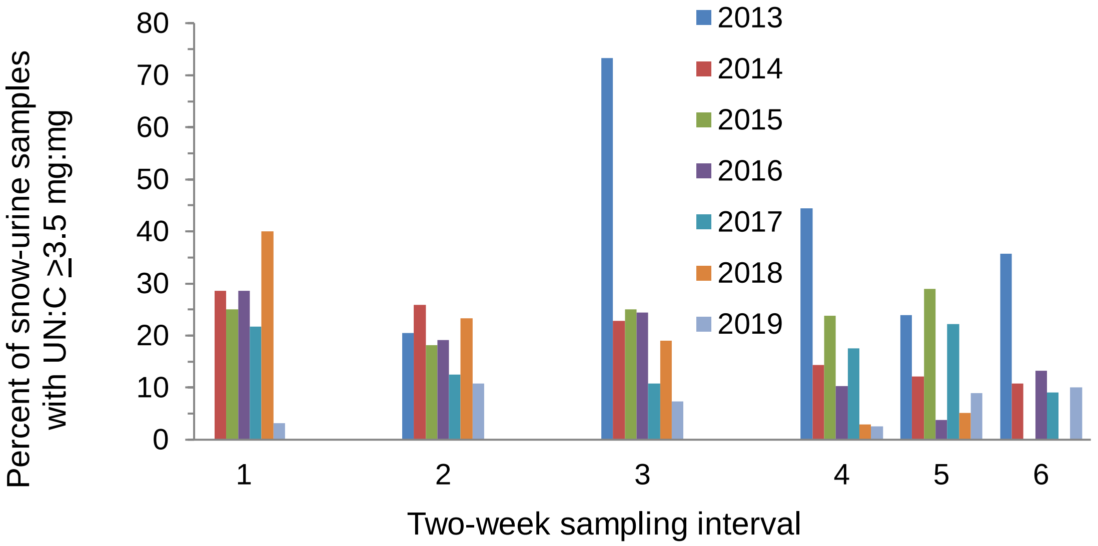

Figure 7. Percent of fresh urine samples voided in snow (snow-urine) by moose and collected during 2-week intervals with urea nitrogen:creatinine (UN:C) ratios indicative of severe nutritional restriction (UN:C ≥3.5 mg:mg) throughout northeastern Minnesota, January–March 2013–2019.

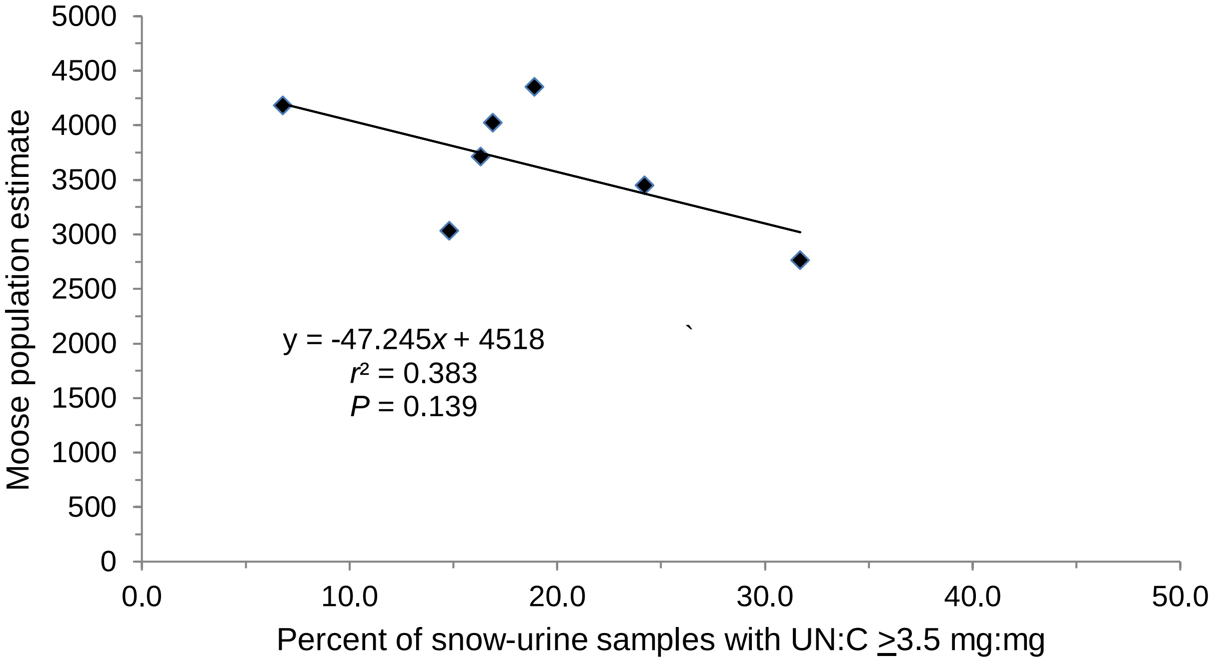

Figure 8. Relationship of the incidence of severe winter nutritional restriction of moose, indicated by the percentage of collected samples of urine in snow (snow-urine) with urea nitrogen:creatinine (UN:C) ratios ≥3.5 mg:mg, to annual population estimates of moose in northeastern Minnesota (estimates from DelGiudice 2018), January–March 2013–2019.

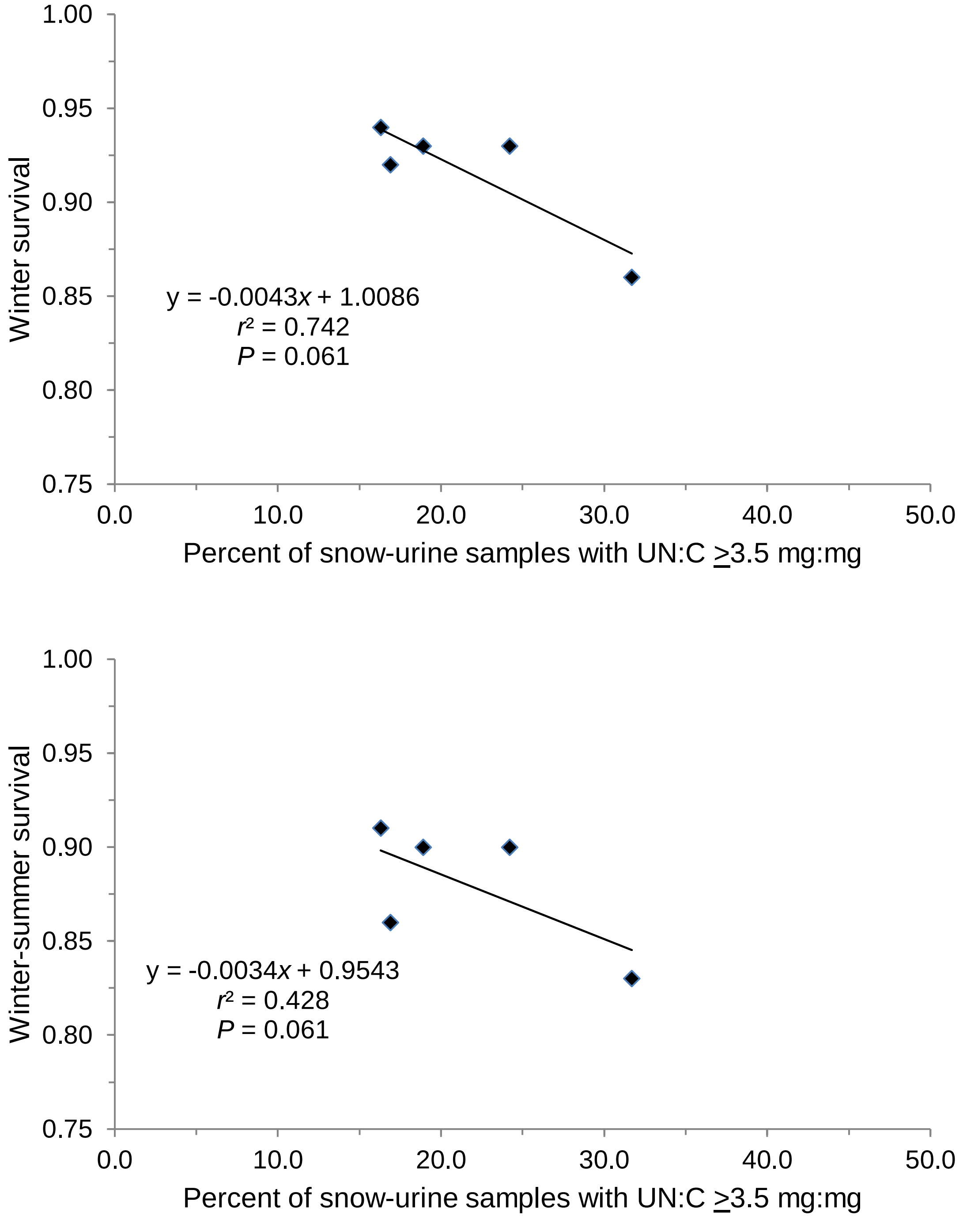

Figure 9. Relationships of the incidence of severe winter nutritional restriction of moose at the population level, indicated by the percentage of collected samples of urine in snow (snow-urine) with urea nitrogen:creatinine (UN:C) ratios ≥3.5 mg:mg, to winter (top, 1 November–31 May 2013−2017) and winter-to-summer (bottom, 1 November–31 August 2013−2017) survival of GPS-collared adult moose in northeastern Minnesota.

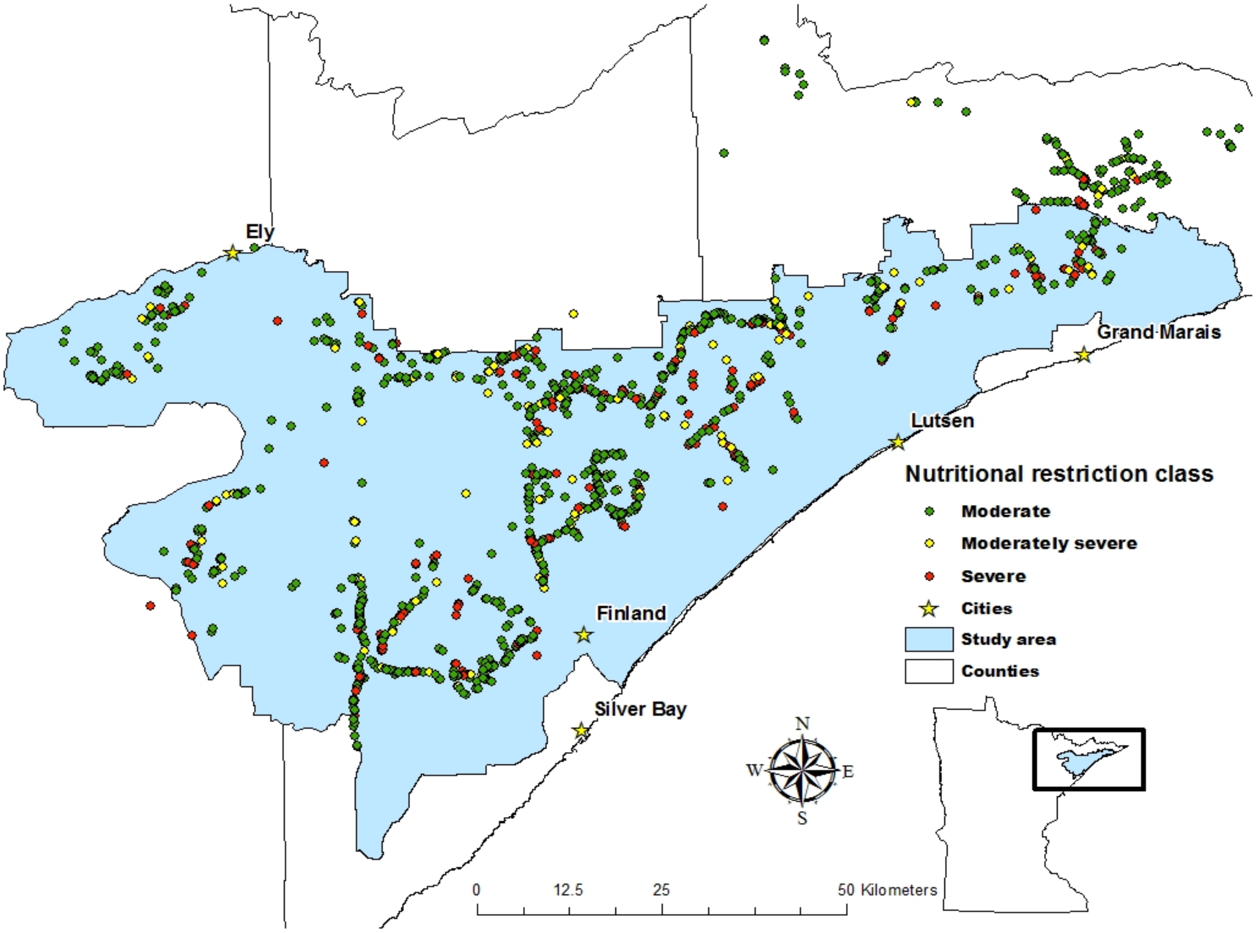

Figure 10. Spatial distribution of 1,479 samples of fresh urine in snow (snow-urine) from moose, serially collected for chemical analysis to assess the severity of winter nutritional restriction. Urinary urea nitrogen:creatinine (UN:C) ratios of <3.0, 3.0–3.4, and ≥3.5 mg:mg are indicative of moderate/normal (white circles), moderately severe (gray circles), and severe (black circles) nutritional restriction in northeastern Minnesota, January–March 2013−2019.