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Patterns in winter nutritional status of white-tailed deer *Odocoileus virginianus* populations in Maine, USA

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We used urinary indices to determine temporal and regional patterns in nutritional status of white-tailed deer *Odocoileus virginianus* in nine wintering areas in northern and central Maine, USA. Winter severity was greater in the northern region, and we expected deer in that region to exhibit greater evidence for nutritional restriction. We collected an average of 26 urine samples from snow on a biweekly basis during 1 January- 31 March 1993 in each wintering area and analyzed them for ratios of urea nitrogen (N):creatinine (C), an index of nutritional status, and potassium (K):creatinine (C), an index of forage intake. Mean urea N:C ratios increased to 3.0 and 3.3 during March in northern and central Maine, respectively, suggesting that nutritional status of deer in these populations was poor. There were no differences in ratios of urea N:C between regions within time periods, except for late March when urea N:C ratios were greater in the central region. The proportions of deer exhibiting severe nutritional restriction (urea N:C ≥ 3.5) were greatest in March in both regions (0.16-0.31); however, proportions were highly variable among populations (range: 0-0.44). K:C ratios decreased during winter, but did not differ among regions. Our results indicate that urinary indices of free-ranging deer populations in wintering areas vary greatly, and we contend that high variability among populations is an important consideration for designing future deer research.

Key words: creatinine, Maine, nutritional status, *Odocoileus virginianus*, potassium, urea nitrogen, urinary metabolites, white-tailed deer

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Traditional approaches for studying white-tailed deer *Odocoileus virginianus* ecology in winter have typically focused on one or a few wintering areas because of logistical constraints of capturing deer or measuring habitat indices. Use of populations or wintering areas as replicate units in larger study designs has generally not

been practical. Techniques based on analyses of metabolites in deer-urine samples collected from snow offer new opportunities for simultaneously evaluating nutritional status of multiple populations because of logistical ease of sampling large numbers of deer. Two indices that have received considerable attention with cap-

tive deer are urea nitrogen (N):creatinine (C) and potassium (K):C ratios (DelGiudice 1995). Urea N:C ratios are influenced by short-term dynamics between energy intake, body-fat depletion and protein catabolism (Parker, DelGiudice & Gillingham 1993), and elevated ratios in winter are indicative of protein catabolism associated with nutritional restriction (DelGiudice, Mech, Seal & Karns 1987). K:C ratios have potential as an indicator of food intake where decreasing K:C suggests decreased food consumption (DelGiudice et al. 1987), though the relationship is weaker for deer on winter browse diets than on commercial feeds (Servello & Schneider 2000).

In this study we examined basic temporal and regional patterns in nutritional status of white-tailed deer populations in Maine, USA. Only one previous study, involving four deer wintering areas in Minnesota, has examined nutritional status of free-ranging white-tailed deer by using urinary indices (DelGiudice, Mech & Seal 1989). We measured urea N:C and K:C ratios in urine samples from nine wintering areas in Maine, five in northern Maine and four in the central region. Because winters are more severe in northern than central Maine, we expected deer in northern wintering areas to exhibit greater evidence of nutritional restriction (greater urea N:C ratios), and we expected evidence for increasing nutritional restriction and decreasing food intake (lower K:C ratios) from early to late winter in both regions.

Material and methods

Study area

We collected deer-urine samples in four deer wintering areas (Tannery, Crossroads, Burlington, Seboeis Stream) in Penobscot Co., Maine (central region) and five wintering areas (Allagash, Schedule Brook, Musquacook, Armstrong, Meadow Brook) in Aroostook Co, Maine (northern region; Fig. 1). All wintering areas were >350 ha in area based on mapped boundaries (Maine Department of Inland Fisheries and Wildlife [MDIFW]), except Meadow Brook, which was approximately 200 ha, although actual areas used by deer were greater than mapped areas. These two regional groups of study sites were approximately 160–200 km apart and occurred in different climatic regions of Maine (Briggs & Lemlin 1992). Central Maine has moderate to severe winters with mean January temperatures of -15°C and average annual snowfall of 180–250 cm (McMahon 1990). Northern Maine has severe winters with mean January temperatures of -19.3°C and average annual snowfall of 258–305 cm (McMahon 1990). Based on a winter severity

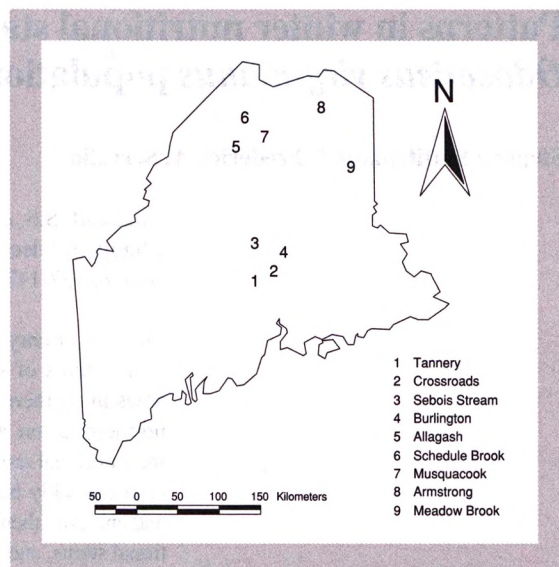


Figure 1. Location of the nine white-tailed deer wintering areas from which samples to evaluate nutritional restriction in Maine, USA, were collected during January–March 1993.

index for deer, severe winters occurred in 8.5 years per decade in the northern region and two years per decade in the central region during 1973–1998 (MDIFW, unpubl. data).

Northern Maine was primarily industrial forestland and largely undeveloped, whereas central Maine was a mix of industrial forestland and clustered residential ownership. Forests in the regions were a mosaic of various-aged regenerating clearcuts, partial harvests, and second-growth hardwood, softwood and mixed-wood stands. Deer wintering areas in both regions were primarily composed of dense stands of balsam fir *Abies balsamea* and spruce *Picea* spp. (Mattfeld 1984). Northern white cedar *Thuja occidentalis* was the predominant tree species in some lowland areas. Topography varied from wet lowlands along drainages to rolling hill terrain, and all wintering areas had some previous timber harvest. Only in the Burlington site had there been recent timber harvesting that left tree tops available for winter food, but this portion of the wintering area was only used by deer during January of our study.

Urine sample collection and analysis

We attempted to collect approximately 25 snow-urine samples from all wintering areas during six time periods (1–15 January, 16–31 January, 1–15 February, 16–28 February, 1–15 March, 16–31 March) in 1993. However, we were unable to collect from some wintering areas in January because snow depths were <5 cm or deer were not present in the wintering area. We made collections

within 120 hours of the most recent snowfall as recommended by DelGiudice & Seal (1988). We attempted to distribute collections throughout each wintering area during each period by searching each wintering area for deer activity, but ultimately collections were spatially distributed relative to deer activity. We collected samples by following tracks of deer, and we limited the number of samples collected to the estimated number of deer in a group to reduce resampling bias. Although we acknowledge the potential for resampling individual deer, we believe resampling was rare and the effects on results were negligible. Biweekly collections from each wintering area were made at intervals of ≥ 1.5 weeks. Samples were stored at -20°C until analyzed (DelGiudice et al. 1989).

Urea N and C concentrations were determined by colorimetric methods using diagnostic kits from Sigma Chemical Co. Potassium concentrations were analyzed by the University of Maine Analytical Laboratory. Ratios of urea N and K to C were calculated on a mg/dL basis for all measurements. Ratios with C are used to control for variability (percent water) associated with single, random urinations and dilution by snow (DelGiudice, Mech & Seal 1988, DelGiudice 1995) because C is excreted according to muscle mass at a constant rate over time (Forbes & Bruining 1976). K:C ratios were multiplied by 100 as in other studies (DelGiudice et al. 1987).

Weather data

We obtained winter climatic data (snow depth, temperature) and deer sinking depth from one weather station in the vicinity of the wintering areas in the northern region and two stations in the vicinity of the wintering areas in the central region. These weather stations were maintained by MDIFW for assessing winter severity for deer. We provide climatic data beginning in mid-December because conditions during this period may influence deer nutritional status during January. Data used were collected at least weekly and temperature data were weekly averages. We calculated weather severity index (WSI) values (Hugie 1973, Lavigne 1992) for each region and biweekly sampling period using data on snow depth, deer sinking depth, and air temperature and long-term (1972-1992) mean temperature data from weather stations. WSI values were computed as:

$$\text{WSI} = (\text{SD}/20 + \text{SK}/18 + (T_{\text{ltm}} - (T_{\text{per}} - T_{\text{ltm}}))/T_{\text{ltm}}) * 33.33$$

where SD is snow depth (inches), SK is deer sinking depth (inches), T_{ltm} is long-term mean temperature, and T_{per} is mean temperature for the period of interest.

For an entire winter, WSI values < 60 are considered mild, 60-74 are moderate, 75-89 are severe, and ≥ 90 are very severe (G.R. Lavigne, MDIFW, pers. comm.) for wintering deer in Maine.

Data analysis

We compared urea N and K:C ratios in northern and central Maine by analyzing data for region, yard within region, period, and period by region interaction effects using 3-factor nested analysis of variance (ANOVA). Urea N:C and K:C ratios were log_e transformed prior to analysis (DelGiudice et al. 1989). We used area within region as the error term for region tests, and area within period as the error term for period. Comparisons

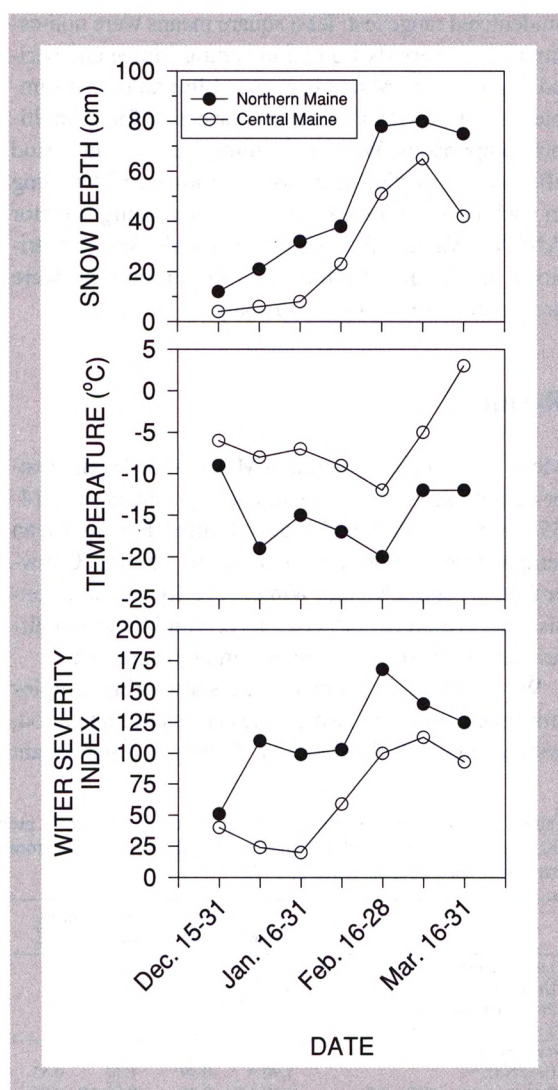


Figure 2. Snow depth, mean air temperature and winter severity index values from weather stations in northern and central Maine during six periods used for deer-urine sampling in January-March 1993.

Table 1. Number (N) of snow-urine samples collected from white-tailed deer in four wintering areas in central Maine and five wintering areas in northern Maine during six sampling periods in January-March 1993.

Wintering area	January		February		March	
	1-15	16-31	1-15	16-28	1-15	16-31
Central Maine						
Tannery	0	0	28	42	42	18
Crossroads	0	0	25	26	32	14
Sebois Stream	18	0	26	38	40	28
Burlington	14	0	53	35	24	23
Northern Maine						
Allagash	33	23	31	8	22	24
Schedule Brook	17	17	25	22	28	23
Musquacook	28	0	34	32	20	30
Armstrong	25	0	20	24	23	12
Meadow Brook	12	12	17	19	9	16

among periods and regions were made using Tukey's studentized range test: least square means were non-estimable for periods 1 and 2 in central Maine and period 2 in northern Maine because of limitations of sample size. We used a Bonferroni correction for all multiple comparisons. We also examined region and period effects on proportion of snow-urine samples ≥ 3.5 mg/mg in each period for each wintering area using 2-factor ANOVA. Values ≥ 3.5 indicate deer under severe nutritional restriction (DelGiudice 1995). Proportions were arcsine-transformed prior to analysis.

Results

Mean snow depths in northern Maine were 23 cm greater than those in central Maine during January and 14-35 cm greater during February-March (Fig. 2). Mean temperatures in northern Maine were 2.5-10.3°C lower than in central Maine. Winter severity also was consistently greater in northern than central Maine, but differences in WSI decreased as winter progressed.

We collected an average of 26 snow-urine samples from each wintering area during each sampling period, with a range of 8-53 (Table 1). There was a significant

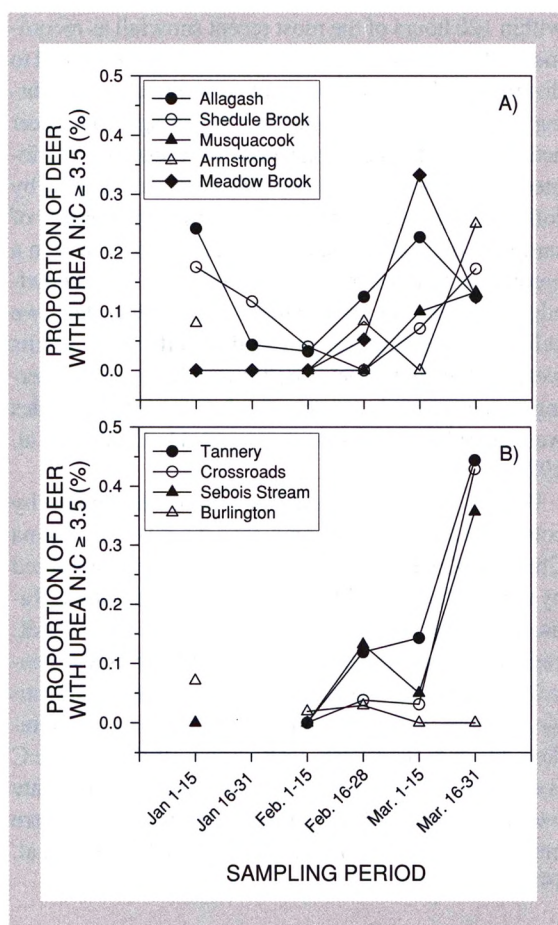


Figure 3. Proportions of snow-urine samples with ratios of urea nitrogen:creatinine (N:C) ≥ 3.5 in biweekly collections from deer wintering areas in northern (A) and central (B) Maine during 1 January - 31 March 1993. The relatively high value in 1-15 March for Meadow Brook (in A) may have been influenced by low sample size (N = 9).

period*region interaction ($F_{4,1086} = 5.22$; $P = 0.001$; Table 2) among urea N:C ratios. However, multiple comparisons indicated that urea N:C ratios increased ($P < 0.05$) from early February to late March in central Maine.

Table 2. Mean urinary urea nitrogen:creatinine ratios (urea N:C), proportions of samples with urea N:C ≥ 3.5 , and postassium:creatinine ratios (K:C) in snow-urine samples from white-tailed deer collected from four wintering areas in central Maine and five wintering areas in northern Maine during January-March 1993.

	1-15 January		16-31 January		1-15 February		16-28 February		1-15 March		16-31 March	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Central Maine												
Urea N:C	1.57	0.83			1.45 Aa	0.09	1.78 Ba	0.25	2.01 Ba	0.33	3.32 Ca	0.74
Proportion urea N:C ≥ 3.5	0.04 A ^a a ^b	0.04			0.01 Aa	0.01	0.08 Aa	0.03	0.06 ABa	0.03	0.31 Ba	0.10
K:C	218	9			170 Aa	19	126 Ba	20	94 Ca	20	96 Ca	9
Northern Maine												
Urea N:C	1.90 A	0.49	1.70	0.55	1.48 Ba	0.12	1.76 Ca	0.20	2.68 Da	0.35	3.02 Db	0.64
Proportion urea N:C ≥ 3.5	0.10 ABa	0.05	0.05 AB	0.04	0.01 Aa	0.01	0.05 ABa	0.02	0.15 Ba	0.06	0.16 Ba	0.02
K:C	249 A	30	273	119	144 Bb	20	160 Bb	30	131 Bb	16	118 Cb	24

^a Mean values in a row with different upper case letters are different ($P < 0.05$).

^b Mean values in a column with different upper case letters are different ($P < 0.05$).

Mean urea N:C ratios increased to >2.0 in early March and >3.0 in late March in both regions, but there were no differences ($P \geq 0.139$) between regions within time periods except during 16-31 March when deer in central Maine had greater ($P = 0.001$) urea N:C in their urine than deer in northern Maine. Proportion of deer with urea N:C ≥ 3.5 differed among periods ($F_{5, 35} = 4.54$; $P = 0.003$), but not between regions ($F_{1, 35} = 0.09$; $P = 0.761$, see Table 2). In northern Maine the proportion of deer with urea N:C ratios ≥ 3.5 were greater ($P \leq 0.031$) in March than in early February, and in central Maine the proportions were greater ($P \leq 0.022$) in late March than in January-February. However, there was considerable variation among wintering areas (range: 0-0.44) in the proportion of deer with urea N:C ratio ≥ 3.5 in late March (Fig. 3). When examining K:C ratios, we detected a period*region interaction ($F_{4, 1074} = 8.43$; $P < 0.001$). Using period-region multiple comparisons we found that K:C ratios decreased ($P < 0.05$) throughout winter in central and northern Maine. K:C ratios were greater ($P < 0.001$) in central Maine during early February and throughout March, but were greater ($P < 0.001$) in northern Maine during late February.

Discussion

Overall winter severity (December 1992 - April 1993) in the wildlife management districts that contained our northern (WSI = 88) and central (WSI = 64) sites was near the long-term average for those districts (northern region: WSI = 92, range: 50-130; central region: WSI = 59, range: 38-86; MDIFW, unpubl. data). Overall WSI values calculated for each region by MDIFW included a greater number of weather stations and more sampling periods than the WSI values we calculated from stations close to our study sites. However, both sets of data were consistent, indicating that our local data accurately represented conditions during the study period.

The 1993 WSI value in the northern region indicated that deer experienced severe conditions and the WSI for the central region indicated moderate wintering conditions (G.R. Lavigne, MDIFW, pers. comm.). Snow depths became increasingly more restrictive to deer activity as winter progressed and likely were a factor in late winter increases in urea N:C ratios. Deep snow greatly increases energetic demands for travel (Mattfeld 1974, Parker, Robbins & Hanley 1984), and there is a substantial increase in costs of locomotion when snow depths exceed 25 cm (Parker et al. 1984). Deer move to winter habitats when snow is 25-48 cm deep (Drolet

1976, Tierison, Mattfeld, Sage & Behrend 1985; G.R. Lavigne, MDIFW, pers. comm.), and depths >55 cm concentrate deer within wintering habitat and restrict travel (Drolet 1976). Mortality rates of deer in northern regions also have been shown to be correlated positively with measures of cumulative days of deep snow (Sauer & Severinghaus 1983, Potvin, Huot & Duchesneau 1981). Potvin et al. (1981) reported mortality rates of 40-50% in Quebec when snow depths exceeded 50 cm for an entire winter (17-18 weeks) or when deep (approximately 80 cm) snow occurred at the end of winter. Snow depths during 1 January - 15 February were <55 cm in both regions in Maine and by this standard would not have concentrated deer activity within wintering areas. Snow depths exceeded 55 cm in the latter half of winter in the northern region and in early March in the central region, and we observed that deer were restricted to trails during these periods.

The proportion of deer exhibiting severe nutritional restriction (urea N:C ratio ≥ 3.5) was greatest during March in both the northern and central regions, likely due to climatic conditions. Ratios ≥ 3.5 indicate that deer are unable to meet energetic requirements by forage intake alone and are relying upon catabolism of body tissues to supplement energetic requirements (Parker et al. 1993, DelGiudice, Mech & Seal 1994). Temporal patterns in urea N:C in our study were generally similar to those reported for deer populations during winter in Minnesota (DelGiudice et al. 1989); however, deer in our study generally had greater mean urea N:C values, particularly in late winter. Maximum snow depths in Minnesota wintering areas ranged within 38-67 cm (DelGiudice et al. 1989) compared to 93 and 95 cm in central and northern Maine, suggesting that winter severity differences may have accounted for greater urea N:C ratios in our study. The presumed decrease in deer nutritional status we observed was consistent with overwinter weight loss reported for deer in northern regions (Moen & Severinghaus 1981, DelGiudice, Mech, Kunkel, Gese & Seal 1992) because of decreased food intake (Holter, Urban & Hayes 1977, Crawford 1982), inadequate dietary energy for maintenance (Gray & Servello 1995), and increased energetic demands for travel in snow (Parker et al. 1984) and cold temperatures (Holter et al. 1977). While our data suggest that there was severe nutritional restriction for 16 and 31% of deer in northern and central Maine, respectively, it is not likely that mortality levels were correspondingly high because deer were confined by snow depths >50 cm (Potvin et al. 1981) and undernourished for a relatively short duration.

The progressive decline in K:C levels suggested that food intake was decreasing in both regions and was a

contributing factor to elevated urea N:C ratios in late winter. DelGiudice et al. (1989) similarly found progressive declines in K:C ratios of deer in four wintering areas in Minnesota. We also found that K:C ratios tended to be greater in central than in northern Maine from February to March, possibly because snow depths were greater in northern Maine and limited access to preferred forages. However, we caution against conclusions on rates of food intake because the K:C ratio-intake relationship has high variability with natural diets (Servello & Schneider 2000).

In contrast to early and mid-winter periods, variability among wintering areas in proportions of deer exhibiting evidence of severe nutritional restriction (urea N:C ratio ≥ 3.5) was high in late winter. We also observed some populations with relatively high proportions of urea N:C ratios ≥ 3.5 in January, and we suspect that this may have been due to use of a wider variety of foods more typical of autumn (Skinner & Telfer 1974, Crawford 1982) which may have had greater protein content. The urea N:C index is only valid for periods when diets are naturally low in protein (DelGiudice 1995), which for white-tailed deer occurs when snow restricts feeding to woody browse. Variability in nutritional status among populations during late winter may be related to a variety of factors including deer density, age structure or habitat characteristics. Region-wide, deer densities were greater in central (4-5 deer/km²) than in northern (1-2 deer/km²) Maine (MDIFW, unpubl. data), which may have influenced rates of browse reduction in wintering areas, and ultimately urea N:C ratios during late winter. However, because deer migrate to wintering areas (Tierson et al. 1985, Nelson 1995), deer densities in individual wintering areas may be influenced by distribution and total area of winter habitat in the region. In northern Maine, deer wintering areas tend to be larger but more widely spaced than in central Maine (G.R. Lavigne, pers. comm.). A second potential influence is variation in proportions of fawns in regional populations. Fawns exhibit the greatest rates of starvation during winter (Sauer & Severinghaus 1983) because they deplete body fat reserves faster than adults (DeCalesta, Nagy & Bailey 1975), and their shorter legs limit mobility and increase energy requirements in snow (Parker et al. 1984). There is evidence for elk *Cervus elaphus* calves to have elevated urea N:C ratios earlier in winter than adults (White, Garrott, Vanderbilt White & Sargeant 1995). The central region of Maine, with its greater densities of deer, may have greater proportions of fawns than the northern region, which may account in part for the lack of expected difference in urea N:C ratios between regions. Lastly, habitat characteristics varied among

wintering areas, particularly as a result of past timber harvesting, which influences physical cover (Ozoga 1968) and food abundance (Wetzel, Wambaugh & Peek 1975, Ditchkoff & Servello 1998).

The number of factors potentially influencing urea N:C ratios of deer populations may explain the lack of a regional difference in urea N:C ratios despite regional differences in winter severity. In retrospect, it may not be reasonable to assume that deer populations will have uniform patterns in nutritional status within a region given the potential variability in population densities, age structure and habitat. There is disagreement on the sensitivity of N:C ratios for detecting nutritional restriction (DelGiudice, Riggs, Mech & Seal 1995, Saltz, White & Bartmann 1995, White, Garrot & Heisey 1997), yet we were able to detect temporal patterns and differences among populations. Our understanding of how the confounding factors listed above influence mean values of urea N:C in a population of deer is poorly understood. However, we feel that this methodology has potential to be a useful tool for assessing condition of deer populations during winter and suggest careful *a priori* planning when designing experiments to examine urea N:C values of wintering ungulates to ensure adequate statistical power (Ditchkoff & Servello 1999).

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