DIFFERENCES IN URINARY CHEMISTRY PROFILES OF MOOSE ON ISLE ROYALE DURING WINTER

Authors: DelGiudice, Glenn D., Peterson, Rolf O., and Seal, Ulysses S.

Source: Journal of Wildlife Diseases, 27(3) : 407-416

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-27.3.407

Journal of Wildlife Diseases, 27(3), 1991, pp. 407–416

DIFFERENCES IN URINARY CHEMISTRY PROFILES OF MOOSE ON ISLE ROYALE DURING WINTER

Glenn D. DelGiudice,[1] Rolf O. Peterson,[2] and Ulysses S. Seal[1,3]

[1] Research Service, Veterans Administration Medical Center, Minneapolis, Minnesota 55417, USA, and Department of Fisheries and Wildlife, University of Minnesota, St. Paul, Minnesota 55108, USA
[2] School of Forestry and Wood Products, Michigan Technological University, Houghton, Michigan 49931, USA
[3] Department of Biochemistry, University of Minnesota, St. Paul, Minnesota 55108, USA

ABSTRACT: During winters 1987–1988 (I) and 1988–1989 (II), we assessed the physiological status of moose (*Alces alces*) residing on the west and east ends of Isle Royale (Michigan, USA) by collecting and chemically analyzing urine deposited in snow (snow-urine) from January to early March. Samples were assayed for urea nitrogen (U), sodium (Na), potassium (K), calcium (Ca), phosphorus (P) and creatinine (C). Throughout both winters, elevated urinary U:C ratios in snow-urine samples collected from east-end moose compared to west-end moose indicated greater dietary energy deprivation and accelerated net catabolism of endogenous protein. Sodium:C ratios were low throughout the study and were similar between moose from both ends of the island, except during the middle of winter I. Greater K:C, P:C and Ca:C ratios in east-end moose compared to west-end moose throughout winter I, and increases in these ratios and U:C in east-end moose from middle to late winter during the second year provided additional evidence of a greater deterioration in condition in east-end moose. The superior nutrition provided to moose on the west end of the island was associated with more developed soils and diverse vegetation and a lower stem density of balsam fir compared to the east end.

Key words: *Alces alces*, electrolytes, moose, nutrition, physiology, potassium, sodium, urea nitrogen:creatinine, urine analysis.

INTRODUCTION

Moose (*Alces alces*) became established on Isle Royale (Michigan, USA) in the early 1900's. This island ecosystem has provided unique research opportunities in moose population dynamics, wolf (*Canis lupus*) predation and habitat relationships for decades (Mech, 1966; Jordan et al., 1971; Krefting, 1974; Peterson, 1977; Belovsky and Jordan, 1981; Peterson et al., 1984; Risenhoover and Peterson, 1986). Isle Royale was declared a National Park in 1940 (Peterson, 1977) to enhance protection of this unique ecosystem. In an effort to minimize the disturbance of moose and preserve the naturalness of the park, capture and handling of moose is rarely permitted. Although much has been learned over past decades about the moose and their important role in this ecosystem, critical understanding of specific aspects of their nutritional ecology has been hindered by the inability to collect physiological data from living animals.

There is an increasing interest by researchers and managers in the identification of physiological indices of condition in free-ranging ungulates. Sensitivity to subtle changes in nutrition and easy accessibility of samples by field biologists are practical and desirable prerequisites of useful indices. Numerous studies have demonstrated nutritional effects on blood constituents in moose and other ungulates (LeResche et al., 1974; Franzmann and LeResche, 1978; Seal, 1978; Hawley and Peden, 1982; Weber et al., 1984; DelGiudice et al., 1987a). Chemical analysis of bladder urine from immobilized ungulates has also been used increasingly to assess metabolic status (Eriksson and Valtonen, 1974; Hove and Jacobsen, 1975; Warren et al., 1981; Waid and Warren, 1984; DelGiudice et al., 1987b, 1990b). However, blood and bladder urine collection require capturing the animals to be sampled, followed by either physical restraint or chemical immobilization. The physical excitement and psychological stress generally associated with these procedures, as well as the chemical immobilizing agents used, can influence concentrations of several blood and urine constituents, thus limiting the usefulness of some data comparisons for evaluating the metabolic status of wild animals (Kock et al., 1987; Seal and Bush, 1987; DelGiudice et al., 1990a). Furthermore, the cost and logistical problems associated with animal capture and sample procurement must be considered (Seal et al., 1981).

Results of habitat and vegetation analyses are used to make indirect inferences concerning the condition of ungulate populations as well (Klein, 1970; Wetzel et al., 1975). However, these methods may also be costly, time-consuming, and lack adequate sensitivity in assessing animal condition for managerial purposes.

During winter, collection and chemical analysis of urine in snow (snow-urine) offers an efficient, practical, and noninvasive alternative to blood and bladder urine analysis and circumvents the aforementioned problems (DelGiudice et al., 1988, 1989a, 1991b). We have shown that ratios of metabolites to creatinine in snow-urine samples accurately represent those ratios in bladder urine (DelGiudice et al., 1988). Furthermore, the sequential collection and analysis of samples, permitted by this technique, greatly facilitates understanding of physiological responses of free-ranging ungulates to nutrition and associated environmental factors (Moen, 1976).

Prompted by obvious differences in soil and vegetation between the east and west ends of Isle Royale (Huber, 1973; Pastor et al., 1988), our objective was to compare chemistry profiles of moose urine on the east and west ends of the island and to assess the physiological status of moose during winters 1987–1988 (I) and 1988–1989 (II).

STUDY AREA

Isle Royale is located in Lake Superior, 24 km from the Canadian mainland (47°55′N, 89°W); the island is 544 km^2 in area, 72 km long and 14 km at its widest point (Peterson, 1977). The highest point on the island is 238 m above Lake Superior. The island is comprised primarily of bedrock strata. The northeastern two-thirds of the island is characterized by thin, azonal soils with numerous bare bedrock ridges. On the western end of the island, soils are thicker, more developed, and consist of abundant deposits of glacial debris (Huber, 1973; Peterson, 1977). Twenty-one of 22 known natural mineral licks on the island occur in areas of glacial till on the west end (Risenhoover and Peterson, 1986). In the absence of moose browsing (which influences soil productivity), soils at the west end have higher nitrogen availability than east end soils (Pastor et al., 1988).

Most of Isle Royale is forested. The east end is "boreal" in character; the west end has an additional mixed "northern hardwood" component (Peterson, 1977). Tree species include sugar maple (*Acer saccharum*), yellow birch (*Betula allegheniensis*), trembling aspen (*Populus tremuloides*), cedar (*Thuja occidentalis*), white birch (*B. papyrifera*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*). Balsam fir and white spruce, and associated stands of white birch and trembling aspen, predominate on the east end of the island (Krefting et al., 1970; Peterson, 1977). Krefting (1974) reported that balsam fir was the most abundant forage species at both ends of Isle Royale; however, mean density was twice as great at the east end compared to the west end. Peterson (unpubl. data) noted stem densities of balsam fir above a 50-cm snow level of 11,000 and 3,800 stems/ha in permanent study plots at the east and west ends, respectively, and similarly, Brandner et al. (1990) found high stem densities of balsam fir primarily at the east end of the island.

Snow depth, similar at both ends of the island, ranged from 40–70 cm and 60–80 cm during winters 1987–1988 and 1988–1989, respectively. Daily maximum ambient temperatures ranged from −12 to 6 C and from −20 to 5 C during January to

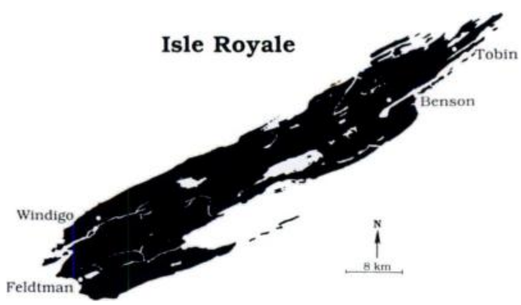

FIGURE 1. Locations of sites on Isle Royale, Michigan, where urine deposited in snow (snow-urine) by moose was collected for physiological assessment of nutritional condition during winters 1987–1988 and 1988–1989.

March 1988 and 1989, respectively; daily minimum temperatures ranged between −29 and −1 C and between −22 and −4 C during these periods (Isle Royale National Park records, Houghton, Michigan 49931, USA).

Winter population estimates of moose on the island were 1,653 ± 224 (95% C.I.) during 1987–1988 and 1,397 ± 211 during 1988–1989 (Peterson, 1988, 1989). Fifty percent of the moose resided on the west and east halves of the island, respectively, and moose densities and calf : cow ratios were similar. Winter movements by moose between the two ends of the island are rare.

MATERIALS AND METHODS

During middle (15 to 27 January) and late winter (5 February to 10 March), we collected snow-urine samples at Windigo (West) and Tobin (East) during both winters to facilitate a comparison of urine chemistry profiles between moose on the ends of the island (Fig. 1). During February 1989, we collected additional samples at Feldtman (West) and Benson (East) (Fig. 1).

We collected snow-urine samples within each of the above 2.6 to 5.2 km^2 sampling areas within 24 to 48 hr of recent snowfalls to estimate urination date and to permit association of metabolic data with specific times during the winter (DelGiudice et al., 1989a). Collectors walked 3.2-km transects; when the transect intersected fresh moose tracks, the collector followed the tracks until locating a urine sample. Snow-urine samples were collected into plastic bags to avoid contamination by skin contact and ground debris (DelGiudice et al., 1988). We are confident that we avoided repeated sampling from the same individual moose during a collection by being selective in choosing the sets of tracks along the transect that we followed and by minimizing the number of samples we obtained along a specific trail relative to the number of moose we were tracking (DelGiudice et al., 1989a). During both winters, track size indicated that samples from calves were uncommon.

Snow-urine samples were kept frozen in the field. Samples were thawed at 22 C in the laboratory, contents were thoroughly mixed and aliquoted into plastic 12 cc tubes with snap-on caps, and stored at −20 C until chemically analyzed (DelGiudice et al., 1989a). Subsequently, we assayed samples for urea nitrogen (U), creatinine (C), calcium (Ca), and phosphorus (P) by spectrophotometry and for sodium (Na) and potassium (K) by flame photometry as described by DelGiudice et al. (1987b, 1988).

The rationale for using ratios of chemistries to C was discussed by DelGiudice et al., (1988, 1991b). Ease of data comparison within this study and with data from other studies was facilitated by multiplying Na:C and K:C ratios by 100 and Ca:C and P:C by 1,000 (DelGiudice et al., 1987b, 1989a, unpubl.). Most chemistry data were $\log_e$-transformed to stabilize the variance prior to analysis by three, two, and one-way ANOVA. Data are presented in text as means and standard error of means.

RESULTS

Overall, mean U:C ($P < 0.001$), Na:C ($P < 0.001$), K:C ($P < 0.0001$), and Ca:C ($P < 0.0001$) ratios were greater in snow-urine samples collected during winter I than during winter II (Tables 1 and 2). There were interaction effects between side of island and winter for Na:C ($P < 0.01$), K:C ($P < 0.0001$), and P:C ($P < 0.001$).

We also noted numerous location (east versus west) effects on snow-urine chemistry ratios. Urinary U:C ratios of moose were greater on the east end of Isle Royale compared to the west end during middle and late winter for both years of the study. Mean Na:C ratios were greater on the east side than on the west side during the middle part of winter I, but these ratios were similar during late winter that year and throughout winter II. Potassium : C, P:C, and Ca:C ratios were greater in moose in the east than in the west throughout winter I, but all three ratios were greater in the

TABLE 1. Comparison of chemistry profiles of urine deposited in snow (snow-urine) for free-ranging moose on the Isle Royale, Michigan, winter 1987–1988.

Location[b] Season[c]	n	Urinary characteristic[a] U:C $\bar{x}$	U:C SE	Na:C ×100 $\bar{x}$	Na:C ×100 SE	K:C ×100 $\bar{x}$	K:C ×100 SE	P:C ×1,000 $\bar{x}$	P:C ×1,000 SE	Ca:C ×1,000 $\bar{x}$	Ca:C ×1,000 SE
West											
Middle winter	10	2.6[d]	0.2	0.44[d]	0.12	150[d]	29	38[e]	2	3,509[f]	176
Late winter	21	2.9[f]	0.2	2.67	2.18	126[g]	14	37[e]	2	4,144[d,h]	212
East											
Middle winter	8	13.6	6.3	3.08	1.74	527	240	180	74	17,255	6,651
Late winter	17	7.7	1.1	1.43	0.32	197	23	122	57	5,521	636
Overall	56	5.8	1.1	1.96	0.85	209	38	83	21	6,361	1,123

[a] U:C = urea nitrogen : creatinine, Na:C = sodium : creatinine, K:C = potassium : creatinine, P:C = phosphorus : creatinine, and Ca:C = calcium : creatinine.

[b] Samples were collected at Windigo on the west end of the island and at Tobin on the east end.

[c] Middle winter = 15–19 January and late winter = 5 February to 1 March.

[d] $P < 0.05$, West versus East.

[e] $P < 0.005$, West versus East.

[f] $P < 0.001$, West versus East.

[g] $P < 0.01$, West versus East.

[h] $n = 20$.

west during the middle part of winter II. Mean K:C and P:C values were similar between the two ends of the island during late winter that year; however, Ca:C continued to be elevated in the west.

There were also changes in urine chemistry ratios in moose from middle to late winter on both ends of Isle Royale. During winter II, U:C ($P < 0.01$), K:C ($P < 0.01$), P:C ($P < 0.005$), and Ca:C ($P < 0.001$) ratios increased ($P < 0.01$) from middle to late winter on the east end; however, no such changes occurred for U:C, K:C, or P:C in moose on the east end during winter I or on the west end during either winter. Calcium : C decreased ($P < 0.02$) from

TABLE 2. Comparison of chemistry profiles of urine deposited in snow (snow-urine) for free-ranging moose on Isle Royale, Michigan, winter 1988–1989.

Location[b] Season[c]	n	Urinary characteristic[a] U:C $\bar{x}$	U:C SE	Na:C ×100 $\bar{x}$	Na:C ×100 SE	K:C ×100 $\bar{x}$	K:C ×100 SE	P:C ×1,000 $\bar{x}$	P:C ×1,000 SE	Ca:C ×1,000 $\bar{x}$	Ca:C ×1,000 SE
West											
Middle winter	10	2.2[d]	0.2	0.83	0.46	127[e]	32	53[e]	7	3,454[f]	219
Late winter	27	2.6[f]	0.2	0.37	0.03	94	9	69	20	4,077[f]	322
East											
Middle winter	12	3.6	0.3	0.29	0.04	59	8	37	3	2,195	165
Late winter	35	4.8	0.2	1.34	0.89	100	8	86	13	2,900	127
Overall	84	3.6	0.2	0.82	0.38	96	6	70	8	3,243	140

[a] Definitions as described in Table 1.

[b] Samples were collected at Windigo and Feldtman on the west end of the island and at Tobin and Benson on the east end.

[c] Middle winter = 26–27 January and late winter = 12 February to 10 March.

[d] $P < 0.005$, West versus East.

[e] $P < 0.05$, West versus East.

[f] $P < 0.001$, West versus East.

middle to late winter in moose on the east end during the first year, but did not change in moose on the west side during either year.

DISCUSSION

During winters I and II, lower, stable U:C ratios (2.2–2.9) of moose on the west side of Isle Royale from January through early March reflected reduced dietary protein intake, increased reabsorption and recycling of urea, and less net catabolism of body protein than in east-end moose (Mould and Robbins, 1981; Schwartz et al., 1987a; Hundertmark et al., 1990). Higher U:C ratios (5.3 ± 0.3, $n = 46$) are reported for four captive moose fed a high protein-high energy diet ad libitum from mid-January to early March (Alaska Department of Game and Fish, unpubl.). Similarly, mean U:C ratios of moose on the west end were also lower than ratios in captive white-tailed deer (*Odocoileus virginianus*) fed high protein diets (DelGiudice et al., 1987b).

DelGiudice et al. (1989a) reported lower U:C and K:C ratios for free-ranging deer in northeastern Minnesota, compared to moose on the west end of the island; ratio values in the deer progressively declined from January to mid-March with increasing snow depths and indicated decreasing food consumption. The snow regime in northeastern Minnesota is similar to that on Isle Royale (DelGiudice et al., 1989a); however, the greater height of moose permits greater mobility in deep snow and facilitates increased access to food (Kelsall, 1969). Deer in northeastern Minnesota consuming natural vegetation, but also with access to a high quality artificial feed, had U:C values during March comparable to ratios in moose on the west side of Isle Royale (DelGiudice et al., 1989a).

During both winters, elevated mean U:C ratios in snow-urine of moose residing on the east end of Isle Royale were indicative of greater dietary energy deprivation and accelerated net catabolism of protein compared to moose at the west end. As with other northern cervids, winter undernutrition of moose is associated with decreased availability and quality of vegetation (Peek et al., 1976; Eastman, 1983), impedence of mobility and feeding by snow cover (Kelsall, 1969; Van Ballenberghe and Peek, 1971; Peek et al., 1976), voluntary hypophagia, decreased energy metabolism, and weight loss (Schwartz et al., 1984, 1987b; Regelin et al., 1985). Body protein is catabolized during all phases of undernutrition in mammals (Forbes, 1985; Torbit et al., 1985; DelGiudice et al., 1990b). When energy is adequate for maintenance in moose and other cervids, urinary excretion of nitrogen (primarily in the form of urea) decreases with reductions in protein intake (Robbins et al., 1974; Hove and Jacobsen, 1975; Mould and Robbins, 1981; Schwartz et al., 1987a); however, progressive negative energy balance and exhausted fat reserves are associated with accelerated endogenous protein degradation (Torbit et al., 1985; Hovell et al., 1987) and increased urinary excretion of urea nitrogen (e.g., U:C ratios) (Wallin, 1979; Waid and Warren, 1984; DelGiudice et al., 1987a, b, 1991a, b; Saltz, 1988). Lower U:C ratios have been documented in free-ranging moose in Denali National Park, Alaska, from January (1.1 ± 0.1, $n = 32$) to March (1.5 ± 0.1, $n = 20$) 1988 (G. D. DelGiudice, unpubl. data) compared to moose at both ends of Isle Royale. Risenhoover (1987) presented evidence of nutritionally superior winter habitat for moose in Denali National Park than on Isle Royale. From Alaska Department of Game and Fish (unpubl.) records (1990) there was a mean U:C of 5.2 ± 0.7 ($n = 7$) in an undernourished moose (29 March to 29 April) that lost 30% of its peak fall weight, and U:C ratios of 17.1 and 36.2 have been reported for two undernourished moose with less than 10% femur marrow fat (DelGiudice et al., 1991a). Mean U:C ratios between 4.0 and 6.0 were observed in captive deer fasted for 2 and 4 wk, and a mean U:C >23.0 occurred in mule deer (*O. hemionus*) that died of winter undernutrition (Saltz, 1988).

There is increasing evidence that urinary U:C ratios approaching 4.0 and higher are indicative of severe nutritional deprivation in deer (DelGiudice and Seal, 1988; Saltz, 1988), moose, and other cervids (DelGiudice et al., 1991a, b; Hundertmark et al., 1990). Because artificial, high quality diets can have direct effects on U:C ratios (DelGiudice et al., 1989a), it is important to be aware of any supplemental feeding when interpreting snow-urine results from a specific area. Isle Royale moose subsisted solely on natural forage, thus facilitating an accurate interpretation of high U:C values and the C ratios of electrolytes associated with them (DelGiudice and Seal, 1988). During winter I, 0.0 and 14.3% of the moose snow-urine samples collected on the west side of the island yielded U:C ratios of 4.0 or greater (4.8 ± 0.1, range = 4.6–5.0) during the middle and late portions of the season, respectively, compared to 37.5 (18.2 ± 9.9, range = 10.5–43.5) and 94.1% (10.1 ± 2.4, range = 5.1–19.0) of the samples from the east end. Maximum U:C ratios in two samples (41.0 and 43.5) from east-end moose during mid-winter suggested exhaustion of fat reserves (DelGiudice et al., 1991a). During winter II, 0 and 3.6% (6.0) of the samples from the west end and 33.3 (4.5 ± 0.2, range = 4.1–4.9) and 66.7% (5.4 ± 0.3, range = 4.1–8.4) of the samples from the east end of the island were indicative of severe energy restriction in moose. From the east end (late winter II), the proportion of samples indicative of severe energy deficiency included 11 of 12 samples from the additional collection site at Benson. The greater percentage of samples reflecting severe energy deficiency on both ends of the island, and greater U:C ratios during winter I compared to winter II, suggested that nutritional deprivation was more severe during the first winter.

Diminished Na:C ratios in snow-urines collected from both ends of the island reflected the reduced Na intake of moose throughout both winters (DelGiudice et al., 1987b). When Na is deficient in the diet, moose, as well as other ungulates, have a great capacity to conserve this element by renal reabsorption and its decreased excretion in urine (Belovsky and Jordan, 1981; Robbins, 1983; DelGiudice et al., 1987b). Sodium is deficient in the diet of moose on Isle Royale between September and May, especially during winter when aquatic vegetation is less available (Botkin et al., 1973; Belovsky and Jordan, 1981). Urinary Na:C ratios in moose on Isle Royale were similar to values in captive deer that were fasted for 4 weeks (DelGiudice et al., 1987b) and to free-ranging moose in Denali National Park during winter (G. D. DelGiudice, unpubl.).

Greatly elevated K:C and P:C ratios in moose on the east end of the island, associated with high U:C ratios throughout winter I, were additional indicators of negative energy balance and/or their depleted fat reserves and their greater dependence on endogenous protein catabolism (Blaxter and Wood, 1951; Tepperman, 1980, p. 253; Torbit et al., 1985; DelGiudice et al., 1987b). The elevated Ca:C ratios in these moose compared to moose on the west end of the island, reflected extensive bone resorption that promoted increased Ca filtration in excess of tubular reabsorption capacity (Gans and Mercer, 1984; DelGiudice et al., 1987b). Flynn et al. (1980) found moose to be in a decreased Ca state during winter. Similar to U:C ratios, K:C and P:C in west-end moose during winter I were more comparable to these ratios in free-ranging deer in northeastern Minnesota during winter (DelGiudice et al., 1989a). Ratios in moose residing on the east side of Isle Royale were far greater than for the deer in Minnesota (DelGiudice et al., 1989a).

During the second year, the lower urinary K:C, P:C, and Ca:C ratios in east-end moose compared to west-end moose during middle winter, that increased with catabolic values of U:C ratios by later winter, suggested progressive deterioration in the condition of moose at the east end of the island. Absence of a change in urinary excretion of metabolites in west-end moose suggested a stable availability of nutrients and a continued sparing of body protein throughout that winter (DelGiudice and Seal, 1988; DelGiudice et al., 1989a, b, 1990b).

Our physiological data clearly suggested a more deteriorated nutritional condition in moose that wintered on the east end of the island compared to the west end during both years of the study. The increase from middle to late winter in the proportion of snow-urine samples collected with U:C values reflecting accelerated catabolism of protein indicated that the apparent nutritional deficiencies were affecting more east-end moose by late winter during both years. However, it was also noteworthy that the disparity in condition between east- and west-end moose did not just become apparent by late winter; rather, a high proportion of moose on the east side of the island appeared to be in poor condition as early as January.

The moose population has been increasing rapidly since the early 1980's, and the estimate of February 1988 (1,653 ± 224) was the highest ever recorded during an aerial census (Peterson, 1988). Although the estimate of 1,397 ± 211 during February 1989 did not represent a statistically significant decline, it at least indicated a cessation in population growth (Peterson, 1989). Physiological data detected severe nutritional deprivation in a portion of the moose population during winter I that was not suspected in an earlier assessment based solely upon the low number of dead moose found during mid-winter and upon fat content of bone marrow collected from those moose. During mid-winter, 16 and 32 moose, killed by wolves, were located during years I and II, respectively (Peterson, 1988, 1989). During both winters, average marrow fat content was between 40 and 60% (Peterson, 1989). However, use of marrow fat content for evaluating nutritional status is a one-way test; low fat content certainly indicates near-exhausted fat reserves and deteriorated condition, but even 100% marrow fat content does not necessarily indicate good condition (Mech and DelGiudice, 1984). Furthermore, carcasses were not surveyed and marrow samples were not collected beyond a 7-week midwinter period (Peterson, 1988, 1989). Most of the winter-kill occurs during March and April (Peterson, 1977; unpubl.); therefore, distribution of the winter-kill over the island is unknown.

There have not been any quantitative assessments comparing winter diets of moose between the two ends of the island. However, it is apparent that the west end comprises a diversity of forest types not found in abundance at the east end. Although the latter supports a greater density of balsam fir, a primary winter forage of Isle Royale moose (Krefting, 1974; Brandner et al., 1990), increased consumption of this species has been associated with major winter die-offs in peak moose populations on the island (Krefting, 1951). Similarly, moose in northeastern Minnesota rely on balsam fir during critical late winter periods (Peek et al., 1976). Elsewhere, moose forage in thinned fir stands more than dense stands (Thompson, 1988), and balsam fir is not regarded as a preferred browse species (Parker and Morton, 1978; Cumming, 1987). Either forage diversity or abundance, or a combination thereof, might explain the differences in moose nutritional status indicated by this study. Collection and chemical analysis of moose urine in snow permitted a direct, sensitive, and quantitative measure of the physiological status of moose on Isle Royale, and clearly showed that the west end of the island with more developed soils and diverse vegetation and a lower density of balsam fir provided superior nutrition compared to the east end of the island. This quantitative measure allows sequential sampling of live moose in specific areas throughout winter and effectively integrates all the complex spatial heterogeneity of forage with other environmental factors (e.g., snow depth) that may potentially influence the nutritional status of moose.

ACKNOWLEDGMENTS

We thank J. M. Thurber and B. Lee-Jameson for their assistance with fieldwork. We are grateful for funding from the National Geographic Society and from the National Science Foundation (BSR-8716095); and for the financial and logistical support of the U.S. National Park Service, Isle Royale; the Veterans Administration Medical Center, Minneapolis, Minnesota; and Michigan Technological University, Houghton, Michigan. We appreciate the technical assistance of M. D. Lewis and S. K. Ruen.

LITERATURE CITED

BELOVSKY, G. E., AND P. A. JORDAN. 1981. Sodium dynamics and adaptations of a moose population. Journal of Mammalogy 62: 613–621.

BLAXTER, K. L., AND W. A. WOOD. 1951. The nutrition of the young Ayrshire calf. 3. The metabolism of the calf during starvation and subsequent realimentation. British Journal of Nutrition 5: 29–55.

BOTKIN, D. B., P. A. JORDAN, A. S. DOMINSKI, H. S. LOWENDORF, AND G. E. HUTCHINSON. 1973. Sodium dynamics in a northern forest ecosystem. Proceedings of the National Academy of Science 70: 2745–2748.

BRANDNER, T. A., R. O. PETERSON, AND K. L. RISENHOOVER. 1990. Balsam fir in Isle Royale National Park, Michigan: Effects of moose herbivory as influenced by density. Ecology 71: 155–164.

CUMMING, H. G. 1987. Sixteen years of moose browse surveys in Ontario. Alces 23: 125–155.

DELGIUDICE, G. D., P. R. KRAUSMAN, E. S. BELLANTONI, M. C. WALLACE, R. C. ETCHBERGER, AND U. S. SEAL. 1990a. Blood and urinary profiles of free-ranging desert mule deer in Arizona. Journal of Wildlife Diseases 26: 83–89.

———, L. D. MECH, AND U. S. SEAL. 1988. Comparison of chemical analyses of deer bladder urine and urine collected from snow. Wildlife Society Bulletin 16: 324–326.

———, ———, AND ———. 1989a. Physiological assessment of deer populations by analysis of urine in snow. The Journal of Wildlife Management 53: 284–291.

———, ———, AND ———. 1989b. Browse diversity and the physiological status of white-tailed deer during winter. Transactions of the North American Wildlife and Natural Resources Conference 54: 134–145.

———, ———, AND ———. 1990b. Effects of winter undernutrition on body composition and physiological profiles of white-tailed deer. The Journal of Wildlife Management 54: 539–550.

———, ———, ———, AND P. D. KARNS. 1987a. Effects of winter fasting and refeeding on white-tailed deer blood profiles. The Journal of Wildlife Management 51: 865–873.

———, ———, ———, AND ———. 1987b. Winter fasting and refeeding effects on urine characteristics in white-tailed deer. The Journal of Wildlife Management 51: 860–864.

———, AND U. S. SEAL. 1988. Classifying winter undernutrition in deer via serum and urinary urea nitrogen. Wildlife Society Bulletin 16: 27–32.

———, ———, AND L. D. MECH. 1991a. Indicators of severe undernutrition in urine of free-ranging elk during winter. Wildlife Society Bulletin 19: 106–110.

———, F. J. SINGER, AND U. S. SEAL. 1991b. Physiological assessment of nutritional deprivation in elk of Yellowstone National Park. The Journal of Wildlife Management 55: In press.

EASTMAN, D. S. 1983. Seasonal changes in crude protein and lignin of ten common forage species of moose in north-central British Columbia. Alces 19: 36–70.

ERIKSSON, L., AND M. VALTONEN. 1974. Seasonal changes in renal urea concentration in the reindeer (*Rangifer tarandus* L.). Annals Zoologica Fennici 11: 200–203.

FLYNN, A., A. W. FRANZMANN, AND C. C. SCHWARTZ. 1980. Seasonal calcium flux in moose. Alces 16: 69–81.

FORBES, G. B. 1985. Body composition as affected by physical activity and nutrition. Federation Proceedings 44: 343–347.

FRANZMANN, A. W., AND R. E. LERESCHE. 1978. Alaskan moose blood studies with emphasis on condition evaluation. The Journal of Wildlife Management 42: 334–351.

GANS, J. H., AND P. F. MERCER. 1984. The kidneys. *In* Duke's physiology of domestic animals, M. J. Swenson (ed.). Comstock Publishing Associates, Division of Cornell University Press, Ithaca, New York, pp. 507–536.

HAWLEY, A. W. L., AND D. G. PEDEN. 1982. Effects of ration, season, and animal handling on composition of bison and cattle blood. Journal of Wildlife Diseases 18: 321–338.

HOVE, K., AND E. JACOBSEN. 1975. Renal excretion of urea in reindeer: Effect of nutrition. Acta Veterinary Scandinavica 16: 513–519.

HOVELL, F. D. DEB., E. R. ORSKOV, D. J. KYLE, AND N. A. MACLEOD. 1987. Undernutrition in sheep. Nitrogen repletion by N-depleted sheep. British Journal of Nutrition 57: 77–78.

HUBER, N. K. 1973. Glacial and postglacial geologic history of Isle Royale National Park, Michigan. Geological Survey Professional Paper 754-A, U.S. Government Printing Office, Washington, D.C., 15 pp.

HUNDERTMARK, K. J., C. C. SCHWARTZ, AND D. C.

JOHNSON. 1990. Evaluation and testing of techniques for moose management. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration Progress Report W-23-3, Juneau, Alaska, 30 pp.

JORDAN, P. A., D. B. BOTKIN, AND M. L. WOLFE. 1971. Biomass dynamics in a moose population. Ecology 52: 147–152.

KELSALL, J. P. 1969. Structural adaptations of moose and deer for snow. Journal of Mammalogy 50: 302–310.

KLEIN, D. R. 1970. Food selection by North American deer and their response to over-utilization of preferred plant species. *In* Animal populations in relation to their food resources, A. Waton (ed.). Blackwell Science Publications, Ltd., Oxford, United Kingdom, pp. 25–44.

KOCK, M. D., D. A. JESSUP, R. K. CLARK, AND C. E. FRANTI. 1987. Effects of capture on biological parameters in free-ranging bighorn sheep (*Ovis canadensis*): Evaluation of drop-net, drive-net, chemical immobilization, and net-gun. Journal of Wildlife Diseases 23: 641–651.

KREFTING, L. W. 1951. What is the future of the Isle Royale moose herd? Transactions of the North American Wildlife Conference 16: 461–472.

———. 1974. The ecology of the Isle Royale moose with special reference to the habitat. Technical Bulletin 297, Forestry Service 15, Agricultural Experiment Station, University of Minnesota, St. Paul, Minnesota, 75 pp.

———, H. L. HANSEN, AND M. P. MEYER. 1970. Vegetation type map of Isle Royale National Park. U.S. Fish and Wildlife Service, U.S. Department of the Interior, Washington, D.C., 1 p.

LERESCHE, R. E., U. S. SEAL, P. D. KARNS, AND A. W. FRANZMANN. 1974. A review of blood chemistry of moose and other cervidae, with emphasis on nutritional assessment. Nature Canada 101: 263–290.

MECH, L. D. 1966. The mammals of Isle Royale. U.S. National Park Service Fauna Series No. 7., Washington, D.C., 210 pp.

———, AND G. D. DELGIUDICE. 1984. Limitations of the marrow-fat technique as an indicator of body condition. Wildlife Society Bulletin 13: 204–206.

MOEN, A. N. 1976. Energy conservation by white-tailed deer in the winter. Ecology 57: 192–198.

MOULD, E. D., AND C. T. ROBBINS. 1981. Nitrogen metabolism in elk. The Journal of Wildlife Management 45: 323–334.

PARKER, G. R., AND L. D. MORTON. 1978. The estimation of winter forage and its use by moose in clearcuts in northcentral Newfoundland. Journal of Range Management 31: 300–304.

PASTOR, J., R. J. NAIMAN, B. DEWEY, AND P. MCINNES. 1988. Moose, microbes, and the boreal forest. Bioscience 38: 770–777.

PEEK, J. M., D. L. URICH, AND R. J. MACKIE. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monograph 48, 65 pp.

PETERSON, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Park Service Scientific Monograph Series No. 11, U.S. National Park Service, Washington, D.C., 210 pp.

———. 1988. Ecological studies of wolves on Isle Royale. Annual Report 1987–88, Michigan Technological University, Houghton, Michigan, 14 pp.

———. 1989. Ecological studies of wolves on Isle Royale. Annual Report 1988–89, Michigan Technological University, Houghton, Michigan, 14 pp.

———, R. E. PAGE, AND K. M. DODGE. 1984. Wolves, moose, and the allometry of population cycles. Science 224: 1350–1352.

REGELIN, W. L., C. C. SCHWARTZ, AND A. W. FRANZMANN. 1985. Seasonal energy metabolism of moose. The Journal of Wildlife Management 49: 388–393.

RISENHOOVER, K. L. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Ph.D. Thesis. Michigan Technological University, Houghton, Michigan, 108 pp.

———, AND R. O. PETERSON. 1986. Mineral licks as a sodium source for Isle Royale moose. Oecologia 71: 121–126.

ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, New York, 343 pp.

———, R. L. PRIOR, A. N. MOEN, AND W. J. VISEK. 1974. Nitrogen metabolism of white-tailed deer. Journal of Animal Science 38: 186–191.

SALTZ, D. G. 1988. Urinary cortisol and urea nitrogen responses to winter stress in mule deer (*Odocoileus hemionus*). Ph.D. Thesis. Colorado State University, Fort Collins, Colorado, 65 pp.

SCHWARTZ, C. C., W. L. REGELIN, AND A. W. FRANZMANN. 1984. Seasonal dynamics of food intake in moose. Alces 20: 223–244.

———, ———, AND ———. 1987a. Protein digestion in moose. The Journal of Wildlife Management 51: 352–357.

———, ———, AND ———. 1987b. Seasonal weight dynamics of moose. Viltrevy (Supplement): 301–310.

SEAL, U. S. 1978. Assessment of habitat condition by measurement of biochemical and endocrine indicators of the nutritional, reproductive, and disease status of free-ranging animal populations. *In* Proceedings of classification, inventory, and analysis of fish and wildlife habitat. Office of Biological Services, U.S. Fish and Wildlife Service, Washington, D.C., pp. 305–324.

———, AND M. BUSH. 1987. Capture and chemical immobilization of cervids. *In* Biology and management of the Cervidae, C. M. Wemmer (ed.). Smithsonian Institution Press, Washington, D.C., pp. 480–504.

———, L. J. VERME, AND J. J. OZOGA. 1981. Physiologic values. *In* Diseases and parasites of white-tailed deer, W. R. Davidson, F. A. Hayes, V. F. Nettles, and F. E. Kellogg (eds.). Miscellaneous Publication 7, Tall Timbers Research Station, Tallahasee, Florida, pp. 17–34.

TEPPERMAN, J. 1980. Metabolic and endocrine physiology. Year Book Medical Publishers, Inc. Chicago, Illinois, 335 pp.

THOMPSON, I. D. 1988. Moose damage to pre-commercially thinned balsam fir stands in Newfoundland. Alces 24: 56–61.

TORBIT, S. C., L. H. CARPENTER, D. M. SWIFT, AND A. W. ALLDREDGE. 1985. Differential loss of fat and protein by mule deer during winter. The Journal of Wildlife Management 49: 80–85.

VAN BALLENBERGHE, V., AND J. M. PEEK. 1971. Radiotelemetry studies of moose in northeastern Minnesota. The Journal of Wildlife Management 35: 63–71.

WALLIN, J. W. 1979. The kidney and the urine. *In* Review of physiological chemistry, H. A. Harper, V. W. Rodwell, and P. A. Mayes (eds.). Lange Medical Publications, Los Altos, California, pp. 626–649.

WAID, D. D., AND R. J. WARREN. 1984. Seasonal variations in physiological indices of adult female white-tailed deer in Texas. Journal of Wildlife Diseases 20: 212–219.

WARREN, R. J., R. L. KIRKPATRICK, A. OELSCHLAEGER, P. F. SCANLON, AND F. C. GWAZDAUSKAS. 1981. Dietary and seasonal influences on nutritional indices in adult male white-tailed deer. The Journal of Wildlife Management 45: 926–936.

WEBER, B. J., M. L. WOLFE, G. C. WHITE, AND M. M. ROWLAND. 1984. Physiologic response of elk to differences in winter range quality. The Journal of Wildlife Management 48: 248–253.

WETZEL, J. F., J. R. WAMBAUGH, AND J. M. PEEK. 1975. Appraisal of white-tailed deer winter habitats in northeastern Minnesota. The Journal of Wildlife Management 39: 59–66.

Received for publication 26 March 1990.