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Overwinter changes in urea nitrogen:creatinine and cortisol:creatinine ratios in urine from Banks Island Peary caribou

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Abstract: Over 200 snow urine samples were collected from Banks Island Peary caribou between March 1993 and May 1998. Most (n=146) samples were collected during 3 time periods in 5 successive years: early winter (3 November-3 December), mid-winter (9 February-1 March), and late-winter (23 April-2 May). We determined the ratios of urea nitrogen:creatinine (U:C) and cortisol:creatinine (C:C) for each sample. U:C ratios had significant year, time, and year x time interaction effects. Mid-winter ratios were higher than early or late-winter ratios. U:C ratios ranged from 0.53 to 19.05 mg/mg, and were lowest in 1997-98. Five calf caribou sacrificed in February 1994 had significantly (P<0.02) higher U:C ratios than other caribou in mid-winter. Three adult male and 2 calf caribou sacrificed in November 1993 had U:C ratios similar to other caribou in early winter. Sacrificed caribou were in similar condition to animals that have been harvested for subsistent use in other years, not overly fat nor in an advanced state of starvation. U:C ratios for Peary caribou range from 10 to *ca.* 100-fold higher than those reported for barren-ground caribou; ratios >60-fold higher than those indicative of prolonged undernutrition in barren-ground caribou were common. This difference is likely because the winter diet of Peary caribou has a higher crude protein content than that of barren-ground caribou. C:C ratios had significant year and year x time interaction effects, and were highest in 1996-97 and 1997-98. C:C ratios of sacrificed caribou were similar to those of other animals during early and mid-winter. C:C ratios for Peary caribou ranged from 0.0120 µg/mg to 0.2678 µg/mg; ratios indicative of morbidity in mule deer were common. C:C and U:C ratios from the same individuals were not correlated (R=-0.073). Monitoring U:C ratios of Banks Island Peary caribou may provide useful management information.

Key words: *Rangifer tarandus pearyi,* snow urine analysis.

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Introduction

The use of the ratios of metabolites from urine voided into snow has become popular for assessing winter nutritional deprivation in ungulates (White *et al.,* 1995; DelGiudice & Seal, 1988). Snow urine samples are obtained and assayed for metabolites such as urea nitrogen and cortisol (DelGiudice *et al.,* 1989; Saltz *et al.,* 1992; Parker *et al.,* 1993), and their levels are reported as ratios with urinary creatinine (Coles, 1980; DelGiudice *et al.,* 1988). A progressive increase in the ratio of urea nitrogen:creatinine (U:C) over winter should occur only when endogenous protein is being catabolized at an accelerated rate (DelGiudice *et al.,* 1987). An increase in the ratio of cortisol:creatinine (C:C) over winter should occur as a result of increased glucocorticoid secretion caused by chronic nutritional deprivation (Saltz & White, 1991).

The collection of snow urine to assess the nutritional status of wild ungulates is of particular utility for low density or endangered populations. DelGiudice & Seal (1988) demonstrated the management value of U:C ratios for white-tailed deer (*Odocoileus virginianus*). They classified deer into three categories of malnutrition: early (U:C <4 mg/mg), prolonged-reversible (U:C 4-<23 mg/mg), and prolonged-irreversible (U:C >23 mg/mg). Subsequently, Case (1996), proposed that U:C >0.25 mg/mg could be used to distinguish barren-ground caribou (*Rangifer tarandus groenlandicus*) which had experienced prolonged undernutrition and remain undernourished.

The Banks Island Peary caribou (*Rangifer tarandus pearyi*) population was estimated at 709±128 (standard error of the mean) ≥1 year-old animals in 1994 (Larter & Nagy, 1997) and has been designated as an endangered population by the Committee on the Status of Endangered Species in Canada (COSEWIC). As part of a comprehensive range study program we wanted to document the levels of snow urine ratios (U:C and C:C) from Peary caribou during the course of the winter to determine if snow urine ratios could have some practical management applicability. We were unwilling to assume that baseline U:C levels determined for barren-ground caribou would necessarily apply to Banks Island Peary caribou because of substantial differences in the basic winter diet. Mould & Robbins (1981) documented that as protein intake increases in elk (*Cervus elaphus*), less urea nitrogen is recycled and urinary urea nitrogen increases. Barren-ground caribou typically have a winter diet dominated by lichen (Klein, 1991) which has a very low protein content (Person, 1975). The winter diet of Banks Island Peary caribou contains substantial proportions of legumes (*Astragalus* spp. and *Oxytropis* spp.) and *Dryas integrifolia*, but virtually no lichen (Larter & Nagy, 1997). Forages in the winter diet of Banks Island caribou have a much higher protein content than lichens, which typically have ≤3% (Soppela *et al*, 1992; N. Larter & J. Nagy, unpubl.). Legumes on the winter range of Banks Island caribou have 11-15% crude protein content (N. Larter & J. Nagy, unpubl.).

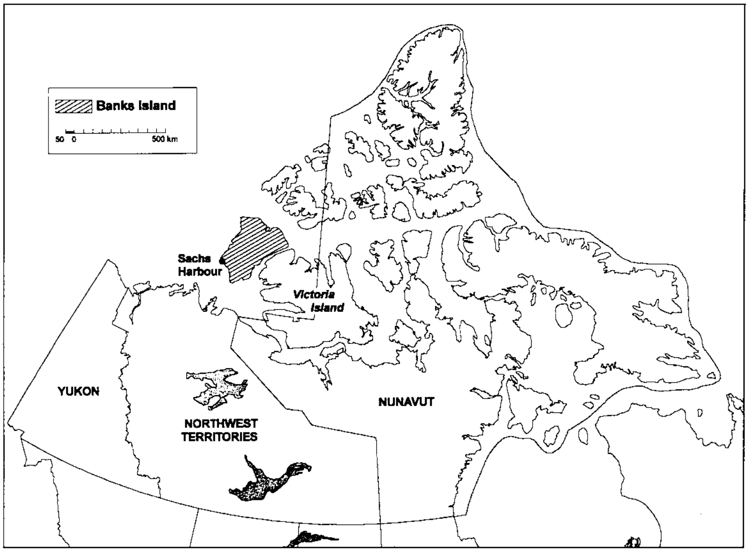

Fig. 1. Northern Canada with Sachs Harbour on Banks Island, Northwest Territories indicated.

In this paper we: 1) document overwinter and annual variation in urea nitrogen:creatinine (U:C) and cortisol:creatinine (C:C) ratios from Banks Island Peary caribou, 2) assess whether the ratios increase over winter as would be expected if increasing nutritional deprivation was occurring, 3) assess whether the ratios are affected by differences in winter snow conditions, and 4) document ratio levels found in different sex and age classes from a small sample of animals from which we had measures of fat reserves and physical condition (Larter & Nagy, 1996).

Study Area

Banks Island is the most western island in the Canadian Arctic Archipelago and covers approximately 70 000 km^2 (Fig. 1). The climate is Arctic Maritime along coastal areas where weather stations are located, tending toward Arctic Desert inland (Zoltai *et al*, 1980). Winters are long, mean monthly temperatures are below 0 °C from September through May, and cold, mean minimum daily temperatures range from -30 to -40 °C from December to March. Summers are short and cool, mean maximum daily temperatures range from 5 to 10 °C from June through August. There is little precipitation, an annual mean of 9 cm (Zoltai *et al*, 1980). Sachs Harbour (population 125) is the only permanent settlement on the island. Zoltai *et al.* (1980) provided a general overview of the geology and glacial history of Banks Island.

Habitat descriptions were adapted from Kevan (1974), Wilkinson *et al.* (1976), and Ferguson (1991). There are 4 major terrestrial habitats: 1) wet sedge meadow, 2) upland barren, 3) hummock tundra, and 4) stony barren. Wet sedge meadows (WSM) are generally level hydric and hygric lowlands characterized by *Carex aquatilis, Eriophorum scheuchzeri,* and *Dupontia fisheri.* Upland barrens (UB) are well drained sites found on the upper and middle parts of slopes. Vegetation is dominated by *Dryas integrifolia* and *Salix arctica.* Hummock tundra (HT) is found on moderately steep slopes and is characterized by individual hummocks which are vegetated primarily by dwarf shrubs (*D. integrifolia, S. arctica,* and *Cassiope tetragona*). Stony barrens (SB) have a coarse gravelly substrate and are sparsely vegetated. This habitat is found on wind blown areas, ridges, and gravel and sand bars. A more detailed description of the flora of Banks Island can be found in Wilkinson *et al.* (1976), Porsild & Cody (1980), and Zoltai *et al.* (1980).

Muskoxen (*Ovibos moschatus*) and Peary caribou (*Rangifer tarandus pearyi*) are the dominant resident herbivores; population estimates from 1994 were 64 608±2009 and 709±128 ≥1 year-old animals of each species respectively (Larter & Nagy, 1997). Other resident herbivores include Arctic hares, ptarmigan and lemmings. During summer there is a substantial population of nesting snow geese (*Chen caerulescens*), which was estimated at 431 000± 48 000 (95% CI) in 1995 (R. Kerbes, pers. comm.). The major resident predators are arctic wolves (*Canis lupus arctos*), polar bears (*Ursus maritimus*), and arctic foxes (*Alopex lagopus*).

Materials and methods

Seven to 14 day field trips were made by snowmobile to research camps located on south central Banks Island during early (3 November-3 December), mid- (9 February-1 March), and late-winter (23 April-2 May). We conducted field trips during winters 1993-94, 1994-95, 1995-96, 1996-97 and 1997-98. During each field trip we collected fresh snow urine samples (≥25 g) left by Peary caribou that were observed during travel. Not all observed caribou provided a sample. An average of 10 samples were collected per trip (range 3 to 20). Samples were kept frozen in individually labelled ziplock bags and transferred frozen to the laboratory in Inuvik at the end of each field trip. We recorded the location of each sample using a global positioning system, and the sex-age class of the caribou that had left the urine sample whenever possible.

In the lab we thawed each frozen urine sample at room temperature and transferred the liquid into 50 ml plastic centrifuge tubes. The liquid in the tube was gently shaken and a subsample of *ca.* 5 ml was pipetted into a 12 x 75 mm tube. This tube was capped and placed in a freezer to refreeze the contents. The remaining liquid in the 50 ml centrifuge tube was stored frozen for backup. Frozen subsamples were shipped to the Veterinary Pathology laboratory at the Western College of Veterinary Medicine, University of Saskatchewan. Urine samples were analyzed for their concentrations of urea nitrogen (mmol/l), creatinine (µmol/l), and cortisol (nmol/l). We converted the values to mg/dL by multiplying urea nitrogen mmol/l by 2.797, creatinine µmol/l by 0.01167, and cortisol, nmol/l by 0.03636 respectively. We present the ratio of urea nitrogen:creatinine (U:C) in mg/mg and the ratio of cortisol:creatinine (C:C) in µg/mg.

Fifty-eight urine samples were collected opportunistically during other field research trips in 1993 and 1998. Samples were collected 21-30 March, 18-20 May, 26-30 October, 4-12 December in 1993, and 22-23 May, 1998. These samples were analyzed as above. Some of the samples collected during November and December 1993 and February 1994 were collected from animals that were sacrificed as part of a caribou collection. Adult male and calf caribou were selected for the collection because it was anticipated that these sex-age classes would be the first to show signs of severe undernutrition (Larter & Nagy, 1996). For each of these animals we collected a urine sample and the following information: sex, age, depth of back fat, kidney fat index (KFI) (following Riney, 1955), visual femur marrow analysis (Riney, 1955) and femur marrow fat content (Neiland, 1970). For a more detailed accounting of the methods see Larter & Nagy (1996).

Starting in winter 1994-95, for each early, mid-, and late-winter field trip we measured snow conditions in the 4 major terrestrial habitats: wet sedge meadow, upland barren, hummock tundra, and stony barren. We measured snow conditions by collecting snow cores to determine snow depth and density, and/or by using a Rammsonde penetrometer (Raillard, 1992; Larter & Nagy, 1994). Ten stations were located along fixed transects in each habitat. At each station we took 2 snow cores, 5 penetrometer measures, and recorded ambient temperature (°C). In winter 1993-94, snow depths and hardness were measured during early and late winter. In March 1993, measurements were limited to depths and densities in wet sedge meadow and upland barren habitats. We used snow measures from upland barrens as indices of relative winter severity for caribou between years, and report mean measures for each time period.

All ratio data were natural-log transformed because snow-urine metabolite ratios are log-normally distributed (White *et al*, 1995). We used an unbalanced ANOVA for two-way design with interaction (proc GLM SAS 6.11 for Windows, SAS

Institute Inc., 1995) to see if there were significant ($P<0.05$) time (early, mid-, late-winter) or year effects on the transformed ratios of U:C or of C:C. If there were significant time or year effects we used the Scheffé multiple comparisons test (proc GLM SAS 6.11 for Windows, SAS Institute Inc., 1995) to see where those differences were. We present the results as median ratios. We used correlation analysis to assess the individual relatedness of the transformed ratios. We used the Mann-Whitney U test to compare U:C and C:C ratios from animals in early, mid-, and late-winter with sacrificed animals, and opportunistic collections during other months.

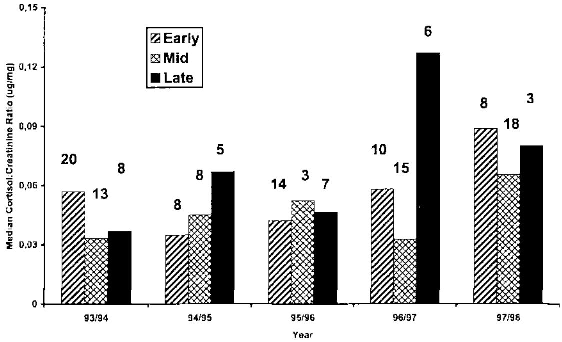

Fig. 3. Median cortisol:creatinine ratios (µg/mg) for all early, mid-, and late-winter periods from winters 1993-94 to 1997-98. Sample size is indicated above each histobar.

Results

The ratios of urea nitrogen:creatinine (U:C) had significant time, year, and time x year interaction effects. Ratios increased or remained fairly constant from early to mid-winter. From mid- to late winter the ratios increased during 3 years, decreased during 1 year, and remained relatively constant during 1 year. Mid-winter values were significantly ($P<0.05$) higher than early and late-winter values, which were similar (Fig. 2). U:C ratios were significantly ($P<0.05$) lower in 1997-98 than in 1996-97, but 1997-98 ratios were similar to 1993-1996 ratios. U:C ratios from the 5 calves sacrificed in February 1994 were significantly ($P<0.02$) higher than ratios determined from other animals during mid-winter (median 14.49, range 7.21-16.86 mg/mg versus median 7.08, range 2.64-17.62 mg/mg). U:C ratios from the 3 males and 2 calves sacrificed in November 1993 were similar ($P>0.05$) to those determined from other animals during early winter (median 8.17, range 3.94-15.76 mg/mg versus 5.54 median, range 1.04-15.83 mg/mg). Although none of the sacrificed animals were fat there were no signs of an advanced state of starvation and they were in similar condition to animals that have been harvested for subsistence use in other years. The nutritional state of calves during winter 1993-1994 must have been adequate because overwinter growth of leg bones was documented in these animals (Larter & Nagy, 1995). U:C ratios ranged from 1.04-15.83 mg/mg during early-winter, 2.64-17.62 mg/mg during mid-winter, and 0.53-19.05 mg/mg during late-winter.

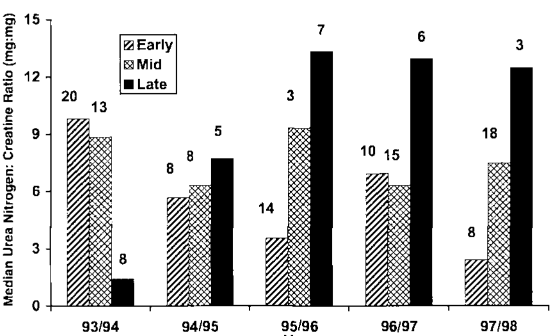

Fig. 2. Median urea nitrogen:creatinine ratios (mg/mg) for all early, mid-, and late-winter periods from winters 1993-94 to 1997-98. Sample size is indicated above each histobar.

The ratios of cortisol:creatinine (C:C) had significant year and time x year interaction effects. Ratios in 1997-98 were significantly ($P<0.05$) higher than those from 1993-1996, but were similar to those in 1996-97 (Fig. 3.). C:C ratios from animals sacrificed in November 1993 and February 1994 were similar ($P>0.05$) to ratios determined from other animals during early and mid-winter (median 0.0873, range 0.0170-0.1532 µg/mg versus median 0.0514, range 0.0120-0.1464 µg/mg and median 0.0356, range 0.0166-0.0892 µg/mg versus median 0.0426, range 0.0157-0.2082 µg/mg, respectively). C:C ratios ranged from 0.0120-0.1532 µg/mg during early-winter, 0.0157-0.2082 µg/mg during mid-winter, and 0.0145-0.2678 µg/mg during late-winter. There was no correlation ($R=-0.073$) between C:C and U:C ratios from the same individuals. The highest recorded C:C ratio was 1.2206 µg/mg from an adult caribou of unknown sex in May, 1998.

U:C ratios recorded in mid-May 1993 were significantly ($P<0.05$) lower (median 1.43, range 0.34-5.73 mg/mg) than those recorded in late-winter or March 1993 (median 13.07, range 8.48-20.93 mg/mg). The lowest ratio recorded was 0.11

mg/mg in mid-May 1998. Ratios in May 1998 (median 0.47, range 0.11-1.34 mg/mg) were similar to those in May 1993 and were significantly lower than ratios in either late winter or March 1993. The highest U:C ratio recorded was 20.93 mg/mg in March 1993. Ratios in March 1993 were all high but were not significantly higher than those recorded for sacrificed animals in February, 1994 (median 14.49, range 7.31-16.86 mg/mg). U:C ratios increased significantly ($P<0.05$) from October 1993 (median 4.77, range 2.28-8.66 mg/mg) to December 1993 (median 9.26, range 6.24-12.43 mg/mg). Ratios in December 1993 were greater than those in early winter and similar to those of sacrificed animals in February 1994 (Fig. 4).

Mean snow depth, snow density, and snow hardness in upland barrens generally increased from early to mid-winter and remained similar from mid- to late-winter (Table 1). The greatest mean snow depth (30.0 cm), and mean snow density (0.401 g/cm^3) in upland barrens were all recorded in March 1993; mean snow hardness was not measured. During winter 1997-98, snow depth, density, and hardness were generally the lowest recorded for each winter period.

Discussion

U:C ratios of Banks Island Peary caribou were low in early winter and increased significantly from early to mid-winter. They were also highest in March, 1993 when snow conditions were the most extreme measured (Table 1). These findings would be expected if endogenous protein was being catabo-

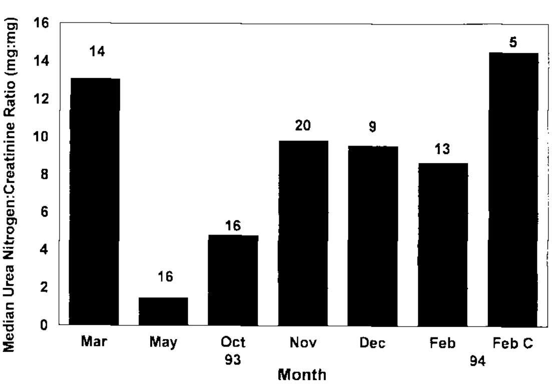

Fig. 4. Median urea nittogen:creatinine ratios (mg/mg) from samples collected between March 1993 and February 1994. The February 1994 histobar includes all samples while the Feb. C histobar documents the median level of only the sacrificed animals. Sample size is indicated above each histobar.

Table 1. Mean (± standard error of the mean) snow depth (cm), snow density (g/cm^3), and snow hardness (number of penetrometer hits) found covering upland barren habitat for all early, mid-, and late-winter periods from winters 1993-94 to 1997-98 and for March 1993. Mean depth (n=70), mean density (n=20) and mean hardness (n=50) unless otherwise noted in parentheses.

	March 1993	1993-94	1994-95	1995-96	1996-97	1997-98
Depth (cm)	30.0±4.5 (5)					
early winter		16.1±0.6 (50)	17.7±1.0	10.1±0.6	11.3±0.7 (68)	6.7±0.6 (62)
mid-winter			21.5±1.4	16.4±0.6	13.2±0.9	8.4±0.6 (65)
late winter		28.2±1.3 (50)	20.3±0.8	13.4±0.7	16.5±1.2	6.2±0.7 (64)
Density (g/cm^3)	0.401±0.016 (5)					
early winter			0.248±0.010	0.257±0.019	0.287±0.017 (18)	0.236±0.015 (12)
mid-winter			0.327±0.016	0.157±0.010	0.245±0.010	0.273±0.016 (15)
late winter			0.306±0.009	0.258±0.010	0.267±0.011	0.199±0.028 (14)
Hardness (# hits)						
early winter		5.6±0.4 (50)	5.4±0.6	1.1±0.2	1.4±0.2	0.8±0.1
mid-winter			17.5±1.6	9.0±2.3	4.8±1.4	4.7±0.6
late winter		20.0±1.8 (50)	10.8±1.1	5.1±0.9	8.5±1.6	3.4±1.0

lized at an accelerated rate as winter progressed (DelGiudice *et al.,* 1987) or winter severity increased, and indicate that information on U:C ratios may provide useful management information. Some of the highest U:C ratios measured were from sacrificed animals that did not show signs of irreversible nutritional deprivation (based upon fat depots), and were generally regarded as being of similar fatness to animals harvested previously by the local residents. Therefore, the range of ratios documented is likely within the normal range experienced by Banks Island Peary caribou. It is unlikely that we reported levels indicative of prolonged-irreversible as reported for barren-ground caribou (Case, 1996) and white-tailed deer *(Odocoileus virginianus)* (DelGiudice & Seal, 1988).

Cortisol is a glucocorticoid that controls the metabolism of energy reserves in animals experiencing chronic stress (Stephens, 1980). One would expect elevated levels when animals have reached the prolonged-irreversible stage of malnutrition. For mule deer C:C ratios of 3 ng/mg reflect normal winter values; values >10 ng/mg suggest high stress and muscle catabolism likely leading to death (Parker *et al.,* 1993). No C:C ratio we measured for Banks Island Peary caribou was <12 ng/mg (high 1220.6 ng/mg). C:C ratios showed little effect of time, year, or winter severity, and showed no correlation with their associated U:C ratios. Levels up to 30-fold greater than mule deer were not fatal, but common in Peary caribou. Unlike the late 1980s and early 1990s, there were no recorded overwinter die-offs of caribou on Banks Island during this 5 year study (Nagy *et al.,* 1996). The animals taken during winter 1993-1994 were taken because of concern that October freezing rains would cause an overwinter die-off of caribou (Larter & Nagy, 1994), but that was not the case. It is likely that the nutritional balance of the animals we have measured over the past 5 years has been adequate and we were unable to measure C:C ratios for animals undergoing any physiological stress because of a low nutritional plane.

Snow conditions were the most extreme measured in March 1993 (Table 1). U:C ratios were highest in March 1993, C:C ratios were not. There was no positive relationship between increasing U:C ratios and increasing winter severity for the other winters although U:C ratios were lowest during the mild winter of 1997-98. There was no relationship between winter severity and C:C ratios whatsoever. C:C ratios were highest in winters 1996-97 and 1997-98 which is puzzling; winter 1997-98 was the mildest winter of the 5 when considering snow conditions (depth, density, and hardness) and forage was more readily accessible. Possibly the lack of any relationship between U:C and C:C ratios indicates that snow conditions over the past 5 years were being well within the norm.

The apparent decrease in U:C ratios from mid- to late-winter could have resulted from, differences in snow dilution, differences in sex-age class composition of the samples, small sample size for late-winter, or from extraordinary late-winter conditions. Snow density tends to be greatest in April. Urine tends to either cut straight through the snow to ground level or to spread out across the top of the snowpack. Snow urine samples in April tend to appear more dilute than at other times of the year. Differences in snow dilution have shown little or no effect in U:C or C:C ratios elsewhere (Saltz & Cook, 1993; White *et al.,* 1995), and we assume that to be the case with our study.

White *et al.* (1995) showed sex-class differences of U:C ratios in elk (*Cervus elaphus*). They warned that the unknown proportions of each sex-age class may influence the mean ratio which is assumed to represent a population measure. We acknowledge that lack complete information on the sex-age class of each sample, but if our analysis had been further partitioned by sex-age classes it would have been of limited utility due to small sample sizes. Different sex-age class composition of the caribou from which samples were collected during each field trip may add additional variability to our estimates. However, we are dealing with a small population, and believe that the samples collected during any time period are a random sample of the population. During each sampling period samples were collected from animals from ≥2 sex-age classes. In retrospect, because the ratios we reported appear to be from the normal range in the winter nutritional plane of Banks Island Peary caribou, variability based upon animal sex-age is less likely to affect the results.

Small sample size and, what appear to be extraordinary values for late-winter 1993-94, have likely played a major role in creating an apparent decrease in U:C ratios from mid- to late-winter. In 1993-94, U:C ratios were significantly (P<0.01) lower in late- than mid-winter. Late-winter 1993-94 ratios were similar to levels found in May 1993 and May 1998, the lowest ratios recorded. In 1995-96, 1996-97, and 1997-98 U:C ratios were higher in late- than mid-winter. In 1994-95 mid- and late-winter U:C ratios were similar. Therefore, in only 1 of 5 late-winter periods have U:C ratios been lower than the previous mid-winter. Late-winter ratios would be expected to remain at or above mid-winter ratios. Samples during late-winter were collected over the shortest time period (10 days). A short term rare event, possibly a recent nutritional event, could have had more effect on the samples than if they were collected over a longer time frame. We have no explanation for such a reduction in ratios. Samples were collected from 3 different sex-age classes from 3 different groups. Snow depth and hardness were relatively greater in late-winter 1993-94 than other years. An increase in the number of late-winter samples will hopefully elucidate this problem and give us a better idea of the overall relationship.

U:C levels for Banks Island Peary caribou ranged from 10 to *ca.* 100 fold higher than those reported for barren-ground caribou from the Bathurst population collected in March (Case, 1996). U:C levels for barren-ground caribou from the adjacent Bluenose population, also collected in March, showed similar levels to those reported by Case (1996), ranging from 0.06 to 1.61 mg/mg (n=24, median 0.40 mg/mg; N. Larter & J. Nagy, unpubl.). Case (1996) proposed that U:C >0.25 mg/mg could distinguish barren-ground caribou which had experienced prolonged undernutrition and remain undernourished. Only 1 of the 204 samples from Banks Island Peary caribou was <0.25 mg/mg. It is unlikely that all sampled individuals were undernourished. The crude protein content of lichen which Bluenose and Bathurst barren-ground caribou subsist on during winter is <3% (Sopella *et al.*, 1992) whereas legumes which are a major constituent of the winter diet of Banks Island Peary caribou has a crude protein content of 11-15% (N. Larter & J. Nagy, unpubl.). Increases in crude protein intake increases urinary urea nitrogen in elk (Mould & Robbins, 1981). One could speculate that the levels proposed by DelGiudice & Seal (1988) to indicate malnutrition in deer: early (U:C <4 mg/mg), prolonged-reversible (U:C 4-<23 mg/mg), and prolonged-irreversible (U:C >23 mg/mg) may be comparable for Banks Island Peary caribou because the crude protein content of the winter browse diet of deer and the winter diet of Banks Island Peary caribou may be similar; only further sampling will tell.

U:C ratios we report for Banks Island Peary were substantially greater than those reported for barren-ground caribou. U:C ratios: 1) increased from early to mid-winter, 2) were highest when winter snow conditions were the most severe, 3) were lowest during the mildest winter, and 4) varied from March 1993 to February 1994 (Fig. 4) as predicted if we assume that forage becomes increasingly difficult to acquire as winter progresses resulting in an accelerated rate of endogenous protein catabolism. C:C ratios we report for Banks Island Peary caribou were substantially greater than those reported for mule deer, but unlike U:C ratios did not vary as predicted if animals were experiencing chronic stress. Some of the highest U:C ratios were recorded from calves sacrificed during mid-winter 1993-94. Based upon fat depots and local knowledge, these animals did not show signs of irreversible nutritional deprivation. Therefore, we lack U:C and C:C ratios determined for animals experiencing severe nutritional stress, and presume that the past 5 winters have not been so severe as to create severe nutritional stress for the population.

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